Pre- and Post Recruitment Processes Determining Dominance by Mussels on Intertidal Reefs in Southern New Zealand

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Abstract

The current explanation for the absence, or low abundance, of filter-feeding invertebrates from some rocky shores is that because of local variation in nearshore oceanographic conditions, larvae do not arrive in sufficient numbers to establish populations. One putative consequence of this is that macroalgae are able to establish dominance in areas where filter-feeders (especially mussels) do not recruit well. While macroalgae have been transplanted to mussel-dominated shores with varying success, the survival, growth and reproduction of transplanted mussels has not been tested in areas dominated by macroalgae.

To determine specifically what tips the balance between shores dominated by filter-feeding invertebrates and those dominated by macroalgae, I monitored the recruitment of intertidal mussels at four sites on the Kaikoura coast: two with mussels present and two algal-dominated. No significant differences in mussel recruitment rates were found between habitats and recruitment intensity at all sites was found to be very low. Recruitment limitation is not the reason for the absence of mussels from algal dominated shores but some form of limitation does occur to reduce the number of arriving mussels.

Predation effects were examined by transplanting juvenile mussels into caged, uncaged and control treatments. No significant differences in predation rates between habitats were found and transplanted mussels in open cages at all sites were removed within 3 days. Mobile fish predators appeared to be the most likely cause of this intense predation.

Growth of transplanted mussels into algal and mussel habitats was found to be significantly different. Mussels grew faster in mussel dominated habitats and after 6 months in algal dominated habitats, all mussels had died.

The outcome of these experiments indicates that there is a close relationship between recruitment, survival and growth which tips the balance and allows the existence of mussel beds along the Kaikoura coastline.

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Chapter 1: General Introduction

The current explanation for the absence or low abundance of filter-feeding invertebrates from some rocky shores is that local variation in nearshore oceanographic conditions prevent larvae from arriving in sufficient numbers to establish or maintain populations (Gaines and Roughgarden 1985, Schiel 2004). One putative consequence of this is that macroalgae are able to establish dominance in areas where filter-feeders, especially mussels, do not recruit successfully (Connolly and Roughgarden 1999). Much of the Kaikoura coastline (South Island, New Zealand) is dominated by macroalgal communities in either wave-exposed and sheltered conditions (Menge et al. 1999, Schiel 2004). Although macroalgae are the dominant habitat-occupiers, there are several sites on this coastline where filter-feeding invertebrates are abundant. The research in this thesis examines whether or not mussels make it to algal areas and if they do, whether they are able to grow and survive. The general goal is to understand why either algae or filter-feeding invertebrates, but usually not both, dominate rocky-shores.

1.1 Background:

For many years ecologists have proposed models explaining the relative importance of biological and physical processes in determining community structure (Kitching et al. 1959, Hairston et al. 1960, Dayton 1971, Paine 1974, Connell and Slatyer 1977, Connell 1978, Sousa 1979, Suchanek 1981, Connell and Sousa 1983, Menge and Sutherland 1987, Menge et al. 1994, Bertness and Leonard 1997, Sherwood and Petraitis 1998, Connolly and Roughgarden 1999). These models of marine community structure have been developed largely from decades of well-researched data on mussel and barnacle communities. Mussel beds are intrinsically complex in terms of their demography, physical structure, associated biota and interactions and so any relationships involving them are thought to be complex (Connell 1970, Menge 1976, Suchanek 1981, Connell 1985, Paine et al. 1985, Barkai and Branch 1988, Petraitis 1991, Seed and Suchanck, Wooton 1993, Possingham et al. 1994).

One of the first population regulation models was proposed by Hairston et al. in 1960. He suggested there was a relationship between methods of population control and the trophic position of a species. The model states that all organisms that fall into the producer, carnivore and decomposer trophic levels are limited by resources and suffer from interspecific competition in a classic, density-dependent manner. Herbivores are seldom food-limited, but are limited instead by predation and are therefore not likely to compete for food resources. In accordance with Hairston's model, mussel populations, because they are classified as filter-feeding omnivores or producers in his model, suffer from interspecific competition and will be limited by their resources (Hairston et al. 1960). However, Hairston's (1960) model is more explicitly aimed at terrestrial populations where omnivory is often considered to be less important. This is not the case in aquatic environments (Menge 2000b). For example, Duffy and Hay (2000) found that omnivory plays a key role in marine communities where the dominance of large brown seaweeds in North Carolina, USA is facilitated by the presence of omnivorous fish that eat grazing invertebrates. Consequently, the applicability of the Hairston model may be limited in the marine environment, as it also does not address the changes in the role of distribution, abundance or diversity at different trophic levels within communities (Menge and Sutherland 1987). More recently, the number of factors in community models has increased to address more specific questions about how species communities and populations are regulated and include competition, predatory distribution and larval supply, intensity of competition, predation and/or disturbance in the regulation of intertidal (Paine 1966, Connell 1978, Menge and Sutherland 1987).

In their models of community structure, Menge and Sutherland) asked two main questions to address the roles of key factors in regulating communities: do patterns of community structure respond predictably to variation in ecological processes (disturbance, competition, and predation), and does the importance of different ecological processes vary predictably in response to variation in environmental conditions (environmental stress and recruitment density)? Within the models, all mobile organisms are considered to be strongly affected by environmental stress, more so than sessile organisms, and food-web complexity decreases with increasing stress.

The Menge and Sutherland (1987) model predicts changes in the importance of biological and physical factors along gradients in recruitment. Under the assumption of high recruitment, the model makes three predictions. In stressful environments consumers have little or no effect as they are absent or inactive and the importance of competition for space is reduced because it takes longer for resource shortages to develop. Both sessile and mobile consumers are regulated by environmental stress and in moderately stressful surroundings consumers are still inefficient, but sessile organisms are less affected by stress and therefore, maintain higher densities leading to a greater competition for space. Finally, in benign environments, consumers limit competition for space unless prey can escape predation and reach high abundances. With a decrease in recruitment density, the importance of competition for a given level of environmental stress is predicted to be lower. Population diversity is also predicted to be lower in harsh environments, because of general intolerance to such conditions. With environmental moderation diversity increases because of the intermediate-disturbance effect in which diversity is greatest when disturbance is neither too rare nor too frequent (Connell 1978).

Many models of community regulation have been tested on rocky intertidal shores and have often focused on the interactions of mussels and barnacles within their communities (Dayton 1971, Paine 1971, 1974, Menge 1976, Connell 1978, Connell and Sousa 1983). As with most marine species, the larvae of mussels and barnacles have an obligate period in the plankton. Studies of both mussels and barnacle populations have shown that sites with higher recruitment intensity have a higher abundance of adult invertebrates and less free space, which is an indication of greater competition (Connolly and Roughgarden 1999, Menge 2000a, Connolly et al. 2001, Forde and Raimondi 2004). However, this is not always the case, and the processes responsible for the variable arrival of sessile invertebrates have been the subject of many studies (e.g. (Kennedy 1977, Barkai and Branch 1988, Anderson and Underwood 1997, Connolly and Roughgarden 1999, Menge 2000a, Bradbury and Snelgrove 2001, Connolly et al. 2001, Gilg and Hilbish 2003).

In general, mussels (Family Mytilidae) are seasonally reproductive, but some populations are known to produce gametes throughout the year (Seed and Suchanck 1992). The time from adult broadcast spawning to juvenile settlement is

up to 3 weeks, depending on the availability of suitable habitat. Mussels are known to settle on a wide variety of filamentous substrata, including the byssal threads of conspecific adults (Bayne 1964), fine branching algae (Seed and Suchanck 1992) and many artificial substances, such as the fibrous ropes used in the myticulture industry and the ovoid Tuffy ^{TM} used by many researchers to quantify mussel recruitment on intertidal shores (Seed and Suchanck, Menge et al. 1994, Rilov and Schiel 2006).

Oceanographic processes are known to affect the transport and arrival of mussel larvae on rocky shores. For example, Menge et al. (1999) suggested that upwelling on the west coast of New Zealand leads to higher concentrations of depth-derived phytoplankton and consequently high mussel recruitment densities. They also suggested that downwelling along the east coast of the South Island could be expected to bring larvae to shore and/or to keep those released there by adults near shore, but would carry weaker swimming larvae and nutrients to deeper depths thus reducing their successful recruitment. However, this contrasts greatly with general upwelling predictions where recruitment in Oregon and California was found to be lower during upwelling events as coastal waters were moved seaward from adult populations (Shkedy and Roughgarden 1997, Connolly and Roughgarden 1999, Chiswell and Schiel 2001, Connolly et al. 2001, Nielson and Navarette 2004, Schiel 2004, Shanks and Brink 2005). Settlement was restricted to episodes of upwelling relaxation or barnacles settled on the offshore rocks or islands, creating a recruitment shadow (Connolly et al. 2001). More recently, Shanks and Brink (2005) at Duck, North Carolina, found that during upwelling conditions, bivalve larvae were not necessarily transported offshore. Movement of larvae during different transport conditions was species-specific and dependent on their vertical position in relation to the thermocline.

The influences of large-scale oceanic conditions on larval transport are further modified by fine-scale local factors on intertidal shores that can affect settlement (Barkai and Branch 1988, Petraitis 1990, Caley et al. 1996, Helson and Gardner 2004). Micro-scale factors include surface roughness, rock cracks, sessile organisms already present, pools, channels, and protected and exposed ledges (Barkai and Branch 1988, Petraitis 1990, Caley et al. 1996, Helson and Gardner

2004). The importance of these factors to successful settlement is further complicated by the behavioural traits of competent larvae, such as primary and secondary settlement and mussel larval preference for settling near adult conspecifics (Bayne 1964, Kennedy 1977, Seed and Suchanck 1992, Buchanan and Babcock 1997)

Behavioural settlement traits were first examined in the mussel *Mytilus edulis* by Bayne (1964). He discovered that *Mytilus* will successively pass from the plankton to the first settlement site, detach and drift until the final, most suitable, settlement place is found. This mechanism was suggested to be an adaptation that could reduce competition between juvenile larvae and adult populations and act as a means of finding the most appropriate habitat for settlement. This research has been supported by many scientists (Bayne 1964, Kennedy 1977, Seed and Suchanck 1992, Buchanan and Babcock 1997).

However, some studies have not seen the role of secondary settlement. On the south east coast of South Africa, Erlandsson and McQuaid (2004) found a positive relationship between adults and recruits of the species *Perna perna* and suggested that juveniles settle directly into adult mussel beds because they create a heterogeneous matrix suitable for juvenile mussel recruitment and survival. However, regardless of the presence or absence of secondary settlement, larval behaviour has important consequences for intertidal community structure, particularly if larvae will not settle in intertidal habitats lacking substantial adult mussel populations.

Following successful recruitment, mussel survival is affected by factors such as food availability (Dahlhoff and Menge 1996, Alunno-Bruscia et al. 2000), competition (Watanabe 1984, Wooton 1993, Petraitis 1995), and predation (Menge 1978, Menge 1983, Barkai and Branch 1988, Robles 1997, Hunt and Schiebling 1998, Petraitis 1998, Connolly and Roughgarden 1999, Patrick 2001). Differences in the quantity of phytoplankton supplied to mussels can significantly impact their survival and growth (Dahlhoff and Menge 1996). For example, Gardner (2000) suggested that mussels may be absent from much of Cook Strait, because of some form of seston (food) limitation. Physiological and biochemical responses in mussels are

known to occur rapidly as nearshore phytoplankton concentrations change, and these bottom-up factors can lead to differences in community structure through changes in predator and prey abundances (Dahlhoff and Menge 1996).

Differences in predation rates can lead to significant variability in many ecosystems, sometimes producing dramatic changes in the abundance and size distribution of prey species and the composition, and species diversity of (Navarette et al. 2005). Two major experimental procedures have been used to attempt to clarify the role of predators in the structure of intertidal communities. The first is manual removal of all predators from an area (Paine 1966). The second is exclusion of predators from selected areas of the shore through experimental treatments (Fairweather et al. 1984). By keeping the density of predators in selected areas at or near zero, both methods allow the effect of predators on the manipulated area to be measured (Fairweather et al. 1984).

One of the first predation experiments was done by Kitching (1959). In this study, mussels were transplanted from wave-swept sites to more sheltered shores and their rate of consumption by crabs and whelks was observed. Mussel beds were successfully formed in sheltered areas where predators appeared to be removed by episodes of oxygen deprivation, and on wave-beaten points where hydrodynamic stress appeared to hinder predator foraging. In these circumstances, physical factors appeared to have some indirect bearing on patterns of zonation by regulating the intensity of predation. These findings suggested that predators may be more susceptible to the physical stress associated with exposed conditions thus creating prey refuges from predation.

The complete predator fauna of temperate intertidal shores is a diverse assemblage of species with a wide variety of foraging adaptations (Robles 1987). A common problem for predators such as sea stars and whelks is that foraging can often be hindered by wave-exposed conditions (Menge 1978). When submerged, these predators are able to forage, but move more slowly and often require longer prey-handling times (Dayton 1971). Prey can accumulate higher on the shore where submergence times are limited, reducing the effect of predation and causing the upper shore to become a spatial refuge from predation (Rilov and Schiel 2006).

These ideas of prey refuge and zonation support the concept that if top-down conditions were changed then significant impacts would be seen on lower trophic levels, but this may depend on environmental conditions.

The effects of exposure on predation and prey-handling times have been examined many times in differing locations (Menge 1976, 1983, Menge and Sutherland 1987, Navarette 1996, Connolly and Roughgarden 1999, Patrick 2001). Menge (1983) suggested that differences in predation intensity over exposure gradients can be attributed to increases in individual predator effectiveness, and to the numbers of individual predators and predatory species. He found that predation by starfish and gastropods in the low shore of exposed sites in New England were negligible. Consequently, *Mytilus edulis* out-competed barnacles (*Balanus*) and algae (*Chondrus crispus*), and dominated space. At sheltered sites, predation levels were high and barnacles and algae were abundant, while sites of intermediate exposure had intermediate predation levels, with a mixed mussel and algal community (Menge 1983). Robles (1987) also found differences in predation rates due to exposure effects on an intertidal rocky shore. He discovered that despite continuous recruitment of small mussels, the shores of Santa Catalina Island, USA, had no mussel beds, and upper shore levels had an extensive cover of perennial algae. In a series of caging experiments he found that lobsters were removing mussels during high tide. However their effects varied across sites of different exposures due to their inability to forage in exposed conditions. These results were paralleled by Osman and Whitlatch (2004) who established from previous studies that, regardless of larval supply, predation by crabs and sea stars on new ascidian recruits in southern New England could potentially control benthic populations. They concluded that while predation on adult mussel species was negligible, the effect of predation on new recruits was substantial enough to result in differences in the development and eventual species composition of the community (Osman and Whitlatch 2004).

In New Zealand, Menge et al. (1999) found predatory invertebrates to be in short supply on east coast shores of the South Island compared to shores on the west coast. The Thaiidid whelk, *Lepsiella scobina*, was found only at mid and high tidal levels, and the low intertidal whelk species, *Thais (Dicathais) orbita* and *Haustrum*

haustorium, were rarely encountered. The seastar *Stichaster australis*, a common predator on west coast shores, was very scarce on east coast shores.

Most recently, Rilov and Schiel (2005) examined landscape-dependent, food-web linkages and the scales of predation and recruitment occurring on rocky intertidal shores in southern New Zealand. They found that when subtidal reefs were present, predation was greater at low shore levels. Predation was more rapid in the low shore than at mid and high shore levels, which was due to a longer foraging time for subtidal predators. They also suggested that despite such intense predation, mussels are able to grow large enough to reach size refuges from fish predation and provide a habitat for recruitment and protection of juvenile settlers.

There is still great debate about the processes that determine habitat dominance on intertidal shores (outlined in Schiel (2004)). My study was prompted by the observations that although mussels are common on some exposed shores, they are largely absent from interspersed platforms dominated by macroalgae. Current hypotheses are that algae persist because of mussel recruitment failure (Connolly and Roughgarden 1999), interference by algae or differential predation among shores (Schiel 2004, Rilov and Schiel 2006). Three main hypotheses were tested by sampling a series of experiments at sites near Kaikoura on the East Coast of the South Island. The first examines whether these shores are dominated by algae because mussel recruitment is limited or are these shores algal dominated as a result of the second hypothesis exploring whether or not mussels are being controlled by greater predation intensity at algal dominated sites. The final hypothesis looks at the idea that if mussels were able to reach algal dominated shores would they be able to survive and grow?

1.2 Study Outline

The research in this thesis is divided into two major components; pre- and post-recruitment processes. Chapter 2 examines how pre-recruitment processes affect the abundance of habitat-forming mussels on algal and mussel dominated reefs. It addresses factors such as habitat structure, larval arrival and the relationship between recruitment and adult abundances around the Kaikoura Peninsula. Post-

recruitment processes affecting these assemblages are addressed in Chapter 3, where the ability of small mussels to withstand predation pressure and their general survival and growth in the two different habitats are examined. Chapter 4 is a general discussion of the research, examining the factors that tip the balance between the dominance of macroalgae or filter-feeding invertebrates in rocky shore assemblages.

2.1 Introduction

This study was done at four sites around the Kaikoura Peninsula on the East Coast of the South Island of New Zealand. Sites were chosen for to their physical and biological similarities, particularly similar rock types, shore height, wave exposure and dominant species assemblages. A generally similar assemblage of benthic invertebrates and macroalgae was found at all sites. *Durvillaea antarctica, Carpophyllum maschlocarpum* and large branching clumps of the green alga *Chaetomorpha coliformis* were the dominant macroalgae. The sea stars *Stichaster australis* and *Astrostole scabra* were the most abundant predators, and the snakeskin chiton *Sypharochiton pelliserpentis* and limpets of the genus *Cellana* and *Siphonaria* were abundant grazers. The major difference between the sites was the presence or absence of mussels. The two mussel sites (Blue Duck and Raramai) contained the four main species of intertidal mussel found throughout New Zealand rocky intertidal habitats: *Mytilus galloprovincialis, Perna canaliculus, Xenostrobus pulex* and *Aulacomya ater maoriana.* The two sites dominated by algae (Black Miller and Slow vehicle bay) were chosen for the noticeable absence of any mussel species.

Black Miller (42º14’07.87”S 173º50’49.23”E) is the most northern site, approximately 35 km north of the Kaikoura Peninsula and is dominated by algae, specifically the bull kelp *Durvillaea antarctica* in the low-shore and coralline turf in the mid-shore. Blue duck (42º16’50.16”S 173º34’62.131”E) is approximately 20 km north of the Kaikoura Peninsula and is dominated by the bull kelp *Durvillaea antarctica*, coralline turf and a mussel bed mostly made up of the endemic green shell mussel *Perna canaliculus*. This site is located on a small headland between two small mountain streams The Blue duck and The Irongate stream. The third site, was named Slow Vehicle Bay (SVB) (42º27’45.32”S 173º32’40.49”E) as no obvious geographic features could be found. It is approximately 15 kms south of the Kaikoura Peninsula, and is dominated by exposed algal assemblages. The final site, Raramai (42º28’29.62”S 173º32’03.41”E) is approximately 18 km south of Kaikoura Peninsula and is dominated by bull kelp, and corallines, and the widely distributed blue mussel *Mytilus galloprovincialis.* These sites

were interspersed over approximately 55 km of coastline and were used to test processes with and without mussels in the presence of macroalgae.

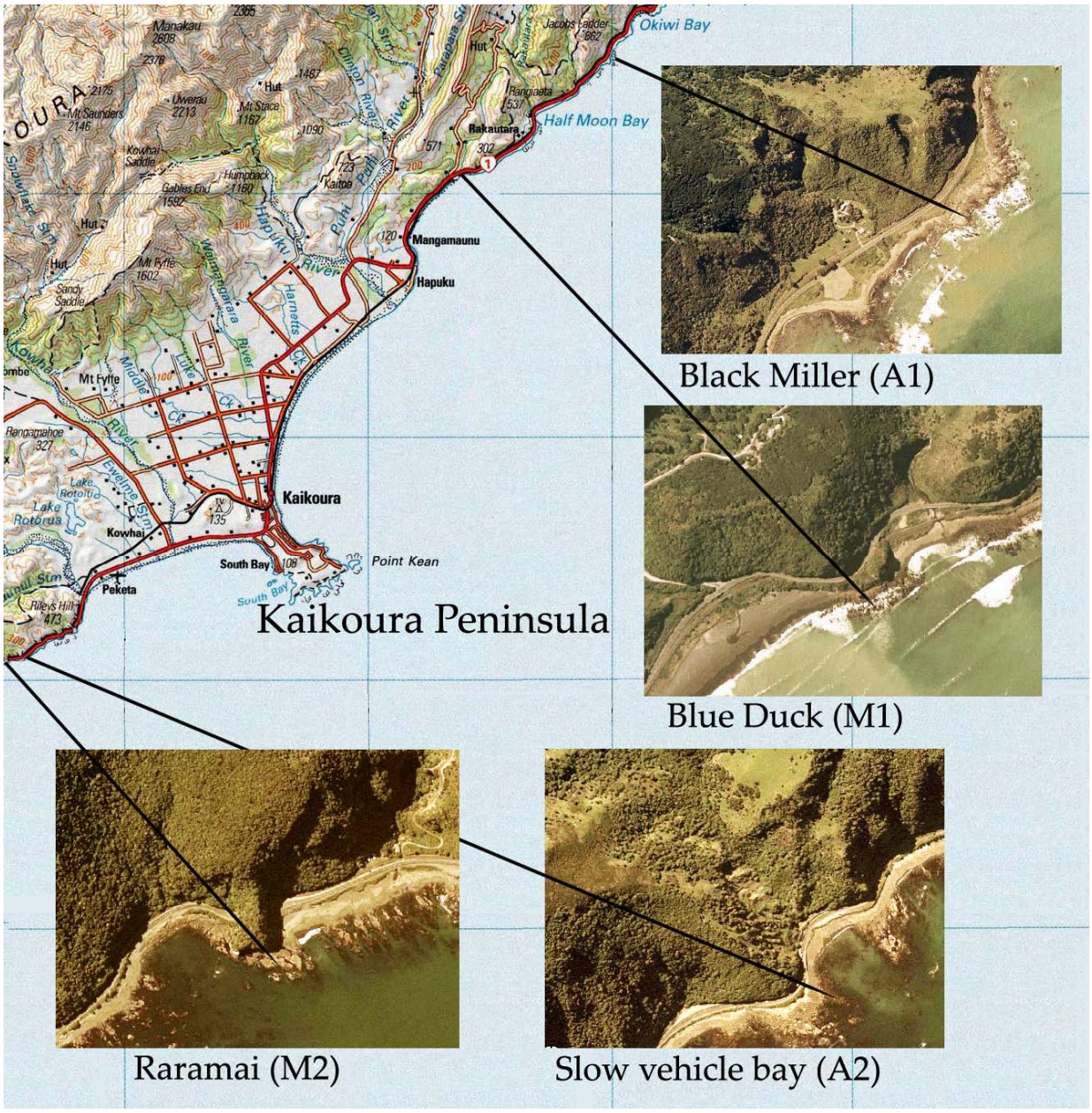

Plate 1.1 Location of study sites around the Kaikoura Peninsula, South Island, New Zealand.

Plate 1.2 Algal habitat; Black Miller (A1), South Island, New Zealand.

Plate 1.3 Mussel habitat; Blue Duck (M1), South Island, New Zealand.

Plate 1.4 Algal habitat; Slow vehicle bay (A2), South Island, New Zealand.

Plate 1.5 Mussel habitat; Raramai (M2), South Island, New Zealand.

2.2 Methods

To examine the magnitudes of wave exposure at each site, maximum dynamometer readings were collected weekly during the New Zealand winter months; June July and August. Maximum wave force was measured at each site over a period of 3 months using dynamometers made to the specifications of (see: Bell and Denny 1994). Dynamometers measure maximum wave force over a sampling period. Measurements were collected weekly for three months over the autumn/ winter months April, May and June. Sea temperature data was kindly provided by the National Institute of Water & Atmospheric Research Ltd (NIWA) for the period October 2004 to December 2006.

Faunal and floral composition at each of the chosen sites was determined by 10 x 1m^2 low shore haphazardly placed quadrats. Percentage cover of algal species and sessile invertebrates were estimated and counts of all mobile invertebrates were done.

2.3 Results

2.3.1 Environmental parameters

A one way ANOVA of mean wave force showed that there was no significant difference between the wave action at each site ($F_{3,44}$=1.352, P=0.27). Blue Duck received the highest mean wave force of 57N followed by Slow vehicle bay at 55N (Figure 2.1).

Measurements relative to the Chart Datum at all sites showed that all low shore study sites were within +/- 0.277m of each other. Blue Duck was the highest site at approximately 0.81m above Chart Datum and Raramai had the lowest low shore zone measured at 0.53m above Chart Datum.

Average monthly sea temperature in Kaikoura ranged from 10ºC to 18ºC from October 2004 until March 2006 (data from the NIWA recording station at the New Wharf in Kaikoura). Air temperature was taken from the same station and show peaks of around 18ºC in the summer and a trough of 10ºC in winter (Figure 2.2).

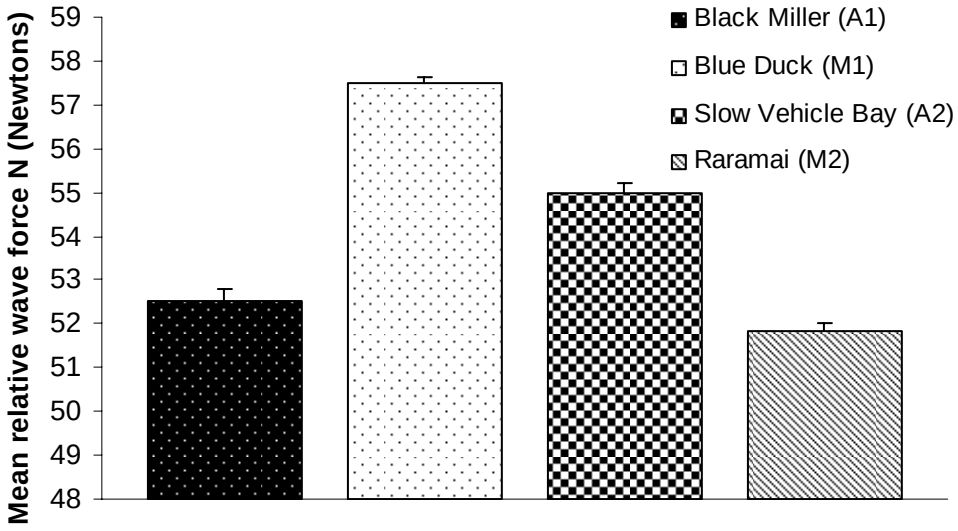

Figure 2.1 Mean relative maximum wave force (N) (± SE) taken from dynamometer readings at both algal (Black Miller, Slow Vehicle Bay) and mussel dominated habitats(Blue Duck, and Raramai).

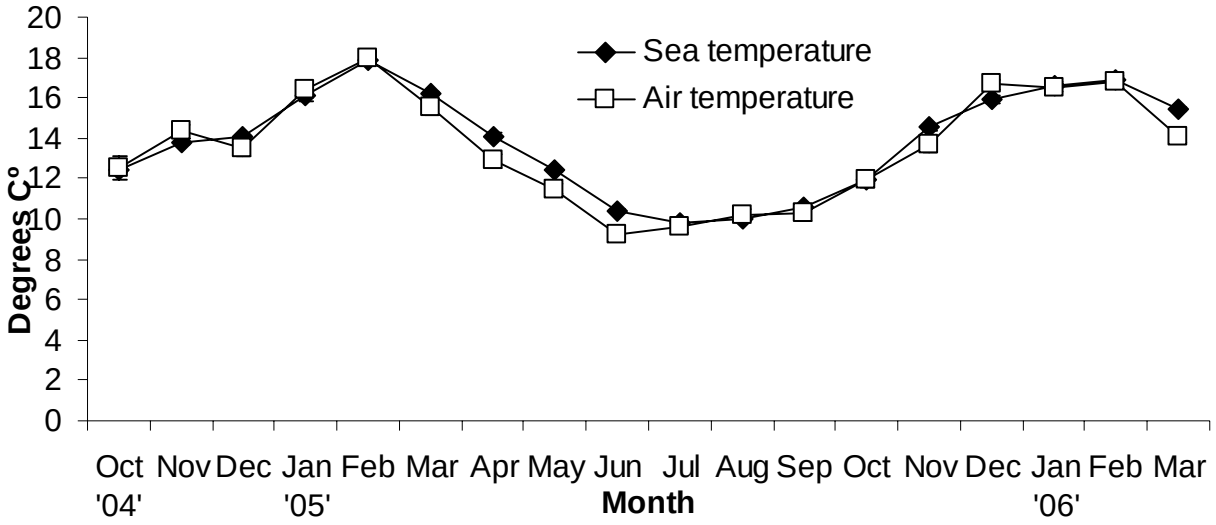

Figure 2.2 Average monthly sea and air temperatures taken from the New Wharf Kaikoura from October 2004 through March 2006.

2.3.2. Community composition

A comparison of dominant organisms between sites within algal and mussel dominated habitats showed that there were similarities between the dominant species of algae and mobile invertebrates at each site. However, mussels were only present at mussel dominated habitats (Figures 2.3 and 2.4)

There were 11 main species or groups that dominated the low-shore zone at both sites within each habitat (Figure 2.3 and 2.4). The most abundant algal species at all sites were the turfing coralline species *Jania microarthrodia* and *Corallina officinialis.* The bull kelp *Durvillaea antarctica* was the dominant fucoid alga on the low shore at all sites but Raramai had a greater cover of *Carpophyllum maschalocarpum* than any of the other sites. There was also a difference in the dominant mussel species at the two mussel sites. Blue Duck had mostly the endemic mussel *Perna canaliculus,* whereas Raramai had mostly the blue mussel *Mytilus galloprovincialis* (Figures 2.3 and 2.4). The small green alga *Chaetomorpha coliformis* was present in the habitats only in the two sites dominated by algae. Bare space was present at Southern sites only, Raramai and Slow Vehicle Bay (SVB).

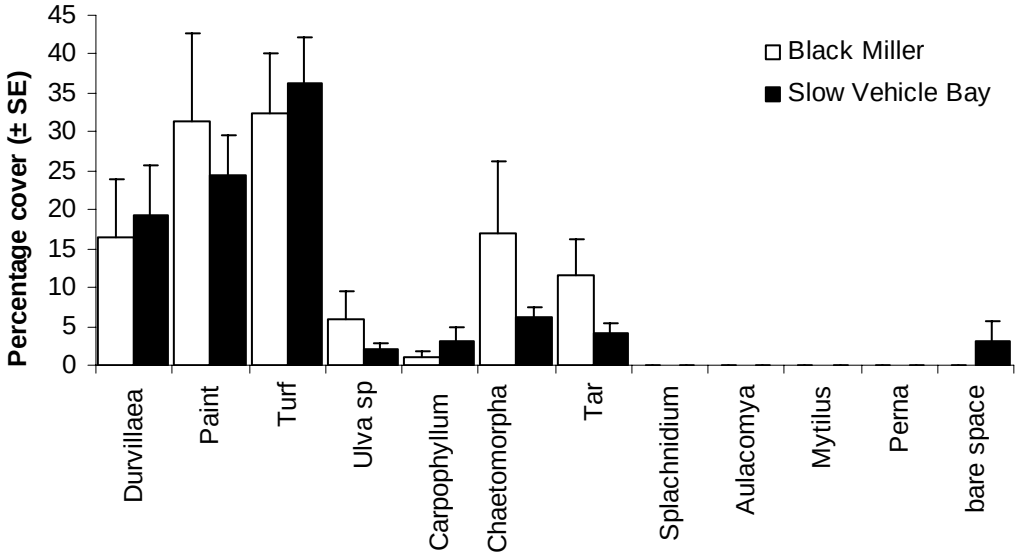

Figure 2.3 Mean percentage cover (± SE) of sessile species in the low shore at the two algal habitats, Black Miller (A1) (white) and Slow vehicle bay (A2) (black). Full species names: *Durvillaea antarctica, Carpophyllum mascholocarpum, Chaetomorpha coliformis, Splachnidium rugosum, Aulacomya ater maoriana, Mytilus galloprovincialis, Perna canaliculus,* and *Chamaesipho* sp. Paint = crust-forming corallines, Tar = crust-forming algae, Turf = turf-forming corallines.

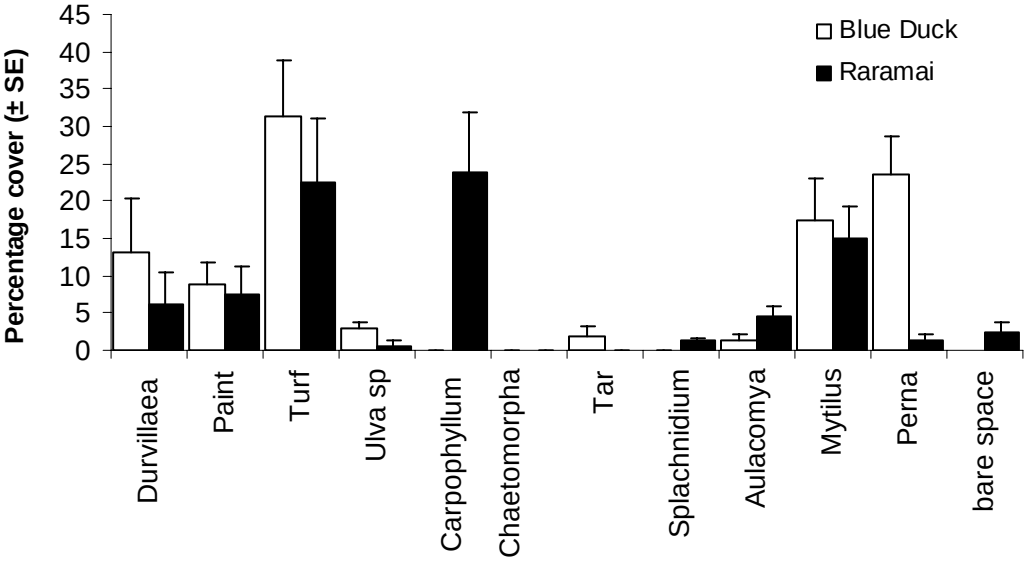

Figure 2.4 Mean percentage cover (± SE) of sessile species in the low shore at the two mussel habitats, Blue Duck (M1) (white) and Raramai (M2) (black). Full species names: *Durvillaea antarctica, Carpophyllum mascholocarpum, Chaetomorpha coliformis, Splachnidium rugosum, Aulacomya ater maoriana, Mytilus galloprovincialis, Perna canaliculus,* and *Chamaesipho* sp. Paint = crust forming corallines, Tar = crust-forming algae, Turf = turf-forming corallines.

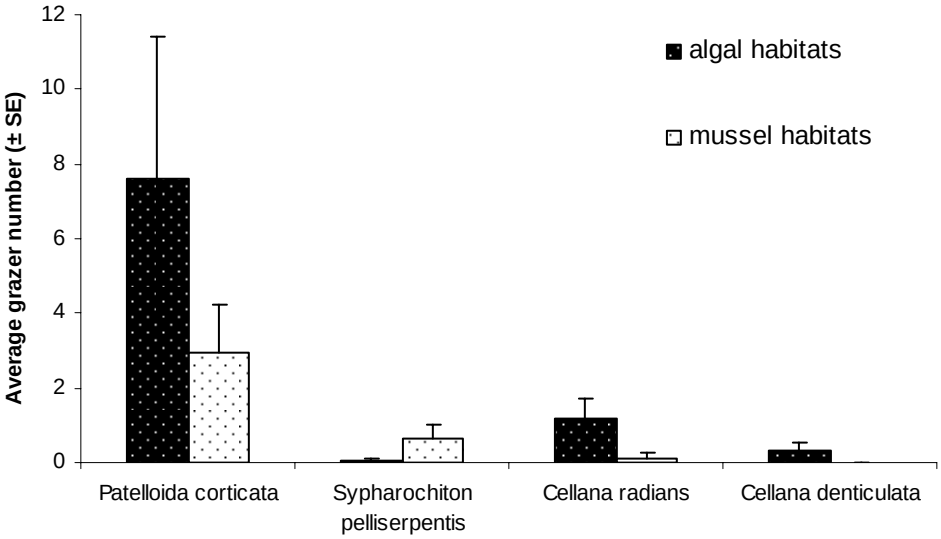

Figure 2.5 Average numbers of limpets (± SE) in low shore quadrats (n= 40) in algal vs. mussel habitats (sites combined within each) Black Miller and SVB (black), Blue Duck and Raramai (white).

Grazing gastropods and predatory whelks were not abundant in the low shore at all sites (Figure 1.5). The small Patellogastropod *Patelloida* was the dominant invertebrate grazer at all sites. Small numbers of the snakeskin chiton *Sypharochiton pelliserpentis* and the Patellid limpets *Cellana radians* and *Cellana denticulata* were also present. Predatory whelks from the low shore areas sampled. These cryptic species may be affected by high wave exposure and may have been taking refuge in small cracks or tide pools.

2.4 Conclusion

Algal species were found to be similar at all sites regardless of the presence or absence of mussels. *P. canaliculus* was the most abundant species in the low shore at Blue Duck and *M. galloprovincialis* was the most abundant at Raramai. Maximum recorded wave-force over the winter months was similar between all sites. Apart from the presence or absence of mussels, all sites were similar in many physical aspects.

3.1 Introduction

Mytilid mussels are a distinctive feature of low to mid-shore intertidal zones worldwide and represent an obvious and vital ecological element of rocky shore communities (Seed and Suchanck 1992). According to Menge et al. (1999) the exposed east coast shores of southern New Zealand have high zones that are dominated by barnacles and mid- and low-shore zones that are dominated by mussels. *Mytilus galloprovincialis* is the spatial dominant, with *Perna canaliculus* as a subdominant. The bull kelp *Durvillaea antarctica* is present only at the extreme low tide mark. Maximum wave-force data for both east and west coasts were comparable indicating that sites with high wave-exposure were generally dominated by filter-feeding mussels rather than algae in the South Island. However, this is not the case in Kaikoura, where many wave-exposed shores are dominated by macroalgae.

On Kaikoura rocky shores there are significant differences between the dominant adult communities that occupy the assemblages. Sites that have seemingly similar environmental conditions (e.g. shore height, wave-exposure) support communities that have different dominant species. Mussels are absent from extensive sections of this coastline despite the presence of seemingly appropriate substrata for settlement. Are these differences in community composition, between algal and mussel dominated habitats, a result of recruitment limitation? Do early mussel settlers make it to algal dominated habitats in the same way they do to mussel dominated habitats?

At another New Zealand location, not far from Kaikoura, two main factors have been examined to explain the absence of mussels from Cook Strait shores. These were recruitment limitation and the low qualities of seston (food) which could cause net energy loss (Gardner 2000, Gardner and Thompson 2001, Helson and Gardner 2004). Wellington harbour, which is only a few kilometres away from Cook Strait, has large populations of mussels, whereas on Cook Strait shores mussels are mostly absent. To test recruitment limitation, larval abundance was estimated via larval pumping and

possible recruitment was examined by using nylon mesh pads attached in the subtidal zone. Larvae were found to be present all year round and higher densities of planktonic mussel were found within the harbour in both pump and collector samples. Although differences in mussel abundance occurred between harbour and coastal sites, the relationship between this and successful settlement is not known. It is for this reason, low seston quality as a means to limit mussel settlement in the Cook Strait was also examined. Prolonged periods of net energy loss were found for *M.galloprovincialis* and this is consistent with their hypothesis that some form of food limitation prevents successful establishment of mussels.

Until recently it was often assumed that organisms with planktonic larval stages had a large larval pool offshore and, therefore, populations were not limited by larval abundance (Pineda 2000). However Doherty (1981), formalised the recruitment-limitation hypothesis, asserting that the planktonic supply of larvae, far from being endless, may often be the limiting factor that affects population size. Consequently, alternate assemblages of species can arise from differences in initial larval supply or from perturbations that sway species densities from one equilibrium point to another (Petraitis 1999). The degree of larval supply to a location and how this abundance relates to the number of mussels that are able to successfully recruit has been examined many times with variable results (Doherty 1981, Roughgarden et al. 1988, Petraitis 1991, Gaines and Bertness 1992, Molares and Fuentes 1995, Nielson and Franz 1995, Caley et al. 1996, Connolly and Roughgarden 1999, Jones et al. 1999, Menge 2000, Schmitt and Holbrook 2000, Connolly et al. 2001, Dudgeon and Petraitis 2001, Lawrie and McQuaid 2001, Helson and Gardner 2004, Broitman et al. 2005).

However, the irregularity and unpredictability of mussel recruitment, and the relationship between larval abundance and successful settlement into a habitat has been difficult to quantify (Purlfrich 1996, Menge 2000, Schiel 2004). To address these issues a variety of artificial spat collectors have been used to assess the abundance of mussel recruits. Mussel recruitment is facilitated by filamentous substrates, a variety of threads, ropes and fibrous mats, as artificial collectors, as they simulate the filamentous nature of some primary algal colonies (Bayne 1964, Paine 1974, Seed and Suchanck

1992). Dudgeon and Petraitis (2001) used rectangular pads cut from furnace filters with a fibrous matrix mimicking patches of algal turf to monitor mussel recruitment. Commercial industries have adopted spat collecting ropes, which are also filamentous (Seed and Suchanck 1992). Another artificial device, a pot scrubber called the 'tuffy' has been compared to the filamentous branching nature of the alga *Endocladia municata* (Paine 1974, Connolly et al. 2001, Menge et al. 2003). It is a standard size, and made of spun plastic, so it is easily replaced and allows useful comparisons between sites and times. The numbers of mussels settling into tuffies may act as an indicator of actual settlement rates into natural areas, tuffies have been used by various researchers (Connolly et al. 2001, Menge et al. 2003, Broitman et al. 2005).

In this chapter I test the hypothesis that pre-recruitment processes in the form of recruitment limitation are responsible for the absence of mussels in algal dominated reefs around Kaikoura. I test this hypothesis through a series of experiments examining mussel recruitment with tuffies and plates in algal and mussel dominated habitats, and investigate whether differences in recruitment to tuffies corresponds with changes in the presence of early settlers in adult mussel beds at mussel dominated sites.

2.2 Methods:

To examine recruitment of mussels at each of two mussel sites and two algal sites (Plate 2.1), five replicate Tuffies ^{TM} (SOS Tuffy pads [The Clorox Company, Oakland, California, USA],) were secured to the low shore with stainless steel 8mm screws (Plate 2.1). These were arranged haphazardly on horizontal rocks at the same tidal height in the low-shore zone. The tuffies were removed weekly and replaced with clean tuffies in the same location. Tuffies were frozen after removal from the shore. To remove invertebrates, they were washed with cold water through a 100μm mesh sieve; tuffies were scanned visually to ensure all recruits had been removed. Samples were then transferred to small plastic vials and preserved with 75% ethanol. This procedure was repeated for 62 consecutive weeks with the first exchange of all tuffies occurring in October 2004. Tuffies were in the field for an average of 7 (± 2) days before exchange. Once preserved, samples were examined under a dissecting microscope using a bokoroff tray and all invertebrates were counted. All mussels were identified to species level (c.f. Booth 1977) and using marine group expertise and all organisms extracted from the tuffy sample were placed into the following categories: gastropods, bivalves, ostracods, amphipods, and isopods and different life history stages of barnacles and crabs.

For comparison of sites across habitats, the total number of mussels of all species recruiting to tuffies at each site was pooled and averaged each week. Homogeneity of variances was analyzed using Cochran's test, but no transformation was found to stabilise the data and remove heteroscedascity. Parametric tests were still used as they are considered robust enough to handle violations of the assumptions of homoscedascity when using large datasets. Cochran's tests of homogeneity of variances were used to assess stability of variances of percentage cover of sessile organisms on carpet plates. Data were arcsine square root transformed to remove heterogeneity (Underwood 1997). Nested ANOVA's (site nested within habitat) of the transformed data was used to assess community composition at each site. Sites were designated as random because of their haphazard locations, and the intention of using

them as replicates within habitats, whereas species and habitats were fixed variables in the ANOVA model.

Ten 10 x 10cm core samples were taken monthly for 7 months (August 2005 - February 2006) from the two mussel dominated sites to compare the composition and size structure of mussel populations. All species of mussel were counted and measured to the nearest millimetre. These counts were made in the field, so any mussels smaller than 500 µm were not included. Factorial ANOVAs were used to test differences between sites in size and abundances of species. The effects of habitat and type of collector (tuffy vs. core) on abundance estimates of recruit size mussels were examined for each species with factorial ANOVA.

Recruitment of algae and mussels to carpet plates was examined in a caging experiment that excluded grazers and predators. Three 10 x 10cm carpet plates (see Rilov and Schiel 2006) were placed into separate cages fastened to the low shore at each of the four sites. After one month they were removed and replaced, and the number, size and species of mussel recruits were recorded as well as the percentage cover of algal species. One-way ANOVAs were used to test if there were significant differences between mussel settlement to carpet plates at mussel and algal habitats in December, January and February 2006.

Plate 2.1 Ovoid tuffy secured to the rocky-shore using an 8mm stainless steel screw.

3.3 RESULTS

3.3.1 Mussel recruitment

There was no significant difference between mussel recruitment into tuffies in algal and mussel dominated habitats (Table 3.1). However, there was a significant difference between sites nested within habitats (Table 3.1). This lack of difference between habitats stems from the variation found within mussel dominated habitats. Raramai had seasonal increases in recruitment that did not occur at Blue Duck. Also recruitment at Blue Duck was consistently less than that found at Slow Vehicle Bay, indicating that mussel recruitment was not limited to habitats already dominated by mussels (Figure 3.1).

Mytilus galloprovincialis had extremely variable recruitment throughout the study period (Figure 3.2). A nested ANOVA of the average number of *M. galloprovincialis* recruits in tuffies through time showed that recruitment varied significantly with time (Table 3.1). Small peaks in recruitment occurred around the end of winter (Aug/Sep) with greater peaks in December (Figure 3.2). These peaks in recruitment were seen at algal and mussel dominated sites. Variation within habitat types was pronounced, with recruitment greater at southern algal and mussel sites (Slow Vehicle Bay and Raramai). *M. galloprovincialis* recruitment was low and variable at all sites, but did not appear to depend on the presence of established adult mussel beds.

Recruitment of *P. canaliculus* was consistently low throughout the year apart from small peaks in April, September and one large peak in December at Raramai (Figure 3.3). Recruitment was not significantly different between habitat types because the small peaks in recruitment were concurrent at algal and mussel dominated sites. However, there was a significant difference in levels of recruitment of *P. canaliculus* through time (Table 3.2). Within habitat differences were largely due to small peaks in recruitment seen at Raramai that did not occur at the other site. *P. canaliculus* recruitment also did not appear to depend on the presence of established mussel beds.

Recruitment of *Aulacomya ater maoriana* followed different seasonal patterns to the other species (Figure 3.4). A greater number of *A.ater maoriana* were found to recruit between February and July 2006. A nested ANOVA showed that there were still significant differences between sites (habitat) and time (Table 3.2). However, for this species the within habitat variation was due to differences between algal rather than mussel dominate sites. Black Miller received a significantly greater number of recruits than Slow Vehicle Bay on most occasions. *A. ater maoriana* recruitment was variable at all sites, but did not appear to depend on the presence of established mussel beds.

Xenostrobus had similar recruitment rates to those found in *P.canaliculus* (Figure 3.5). The greatest peak in recruitment occurred in December at Raramai, with small peaks occurring at Slow Vehicle Bay in December 2004 and September 2005 (Figure 3.5). These seasonal recruitment patterns were reflected in the significant time factor in the nested ANOVA (Table 3.2). There was a large amount of variation between sites within both habitats and *Xenostrobus* recruits did not appear preferentially settle into mussel dominated habitats.

Table 3.1 ANOVA of the average sum of all mussel species recruiting into five tuffies at each site. Pooled mussel species: *Mytilus galloprovincialis, Perna canaliculus, Xenostrobus pulex,* and *Aulacomya ater maoriana*. Weeks and habitats were fixed and site was random.

Source of variance	df	SS	MS	F	P
Weeks	61	7322.26	120.037	5.728	0.000***
Habitat	1	433.72	433.716	2.698	0.242
Site (Habitat)	2	321.49	321.490	7.670	0.000***
Error	1175	24624.07	20.957		

Cochran's test was significant
(significance: * = 0.05, ** = 0.01, *** = 0.001)

Table 3.2 Nested analyses of variance (habitat nested within site) of the effect of time in weeks (n=61), site (n=4) and habitat nested within site (n=2) on the recruitment of A) *Mytilus galloprovincialis*, B) *Perna canaliculus*, C) *Aulacomya ater maoriana*, and D) *Xenostrobus pulex*. Site are treated as random, all other factors are fixed.

A) *Mytilus galloprovincialis*

Source of variance	**df**	**MS**	**F**
Time	61	13.486	**6.871**
Habitat	1	42.587	4.813
Site (Habitat)	2	8.849	**4.508**
Error	1175	1.963	

B) *Perna canaliculus*

Source of variance	**df**	**MS**	**F**
Time	61	13.538	**5.494**
Habitat	1	15.116	0.629
Site (Habitat)	2	24.039	**9.755**
Error	1175	2.464	

C) *Aulacomya ater maoriana*

Source of variance	**df**	**MS**	**F**
Time	61	6.979	**13.349**
Habitat	1	13.107	3.238
Site (Habitat)	2	4.048	**7.743**
Error	1175	0.523	

D) *Xenostrobus pulex*

Source of variance	**df**	**MS**	**F**
Time	61	23.105	**4.661**
Habitat	1	40.162	0.905
Site (Habitat)	2	44.377	**8.952**
Error	1175	4.957	

Cochran's tests were significant
Bold = significant result

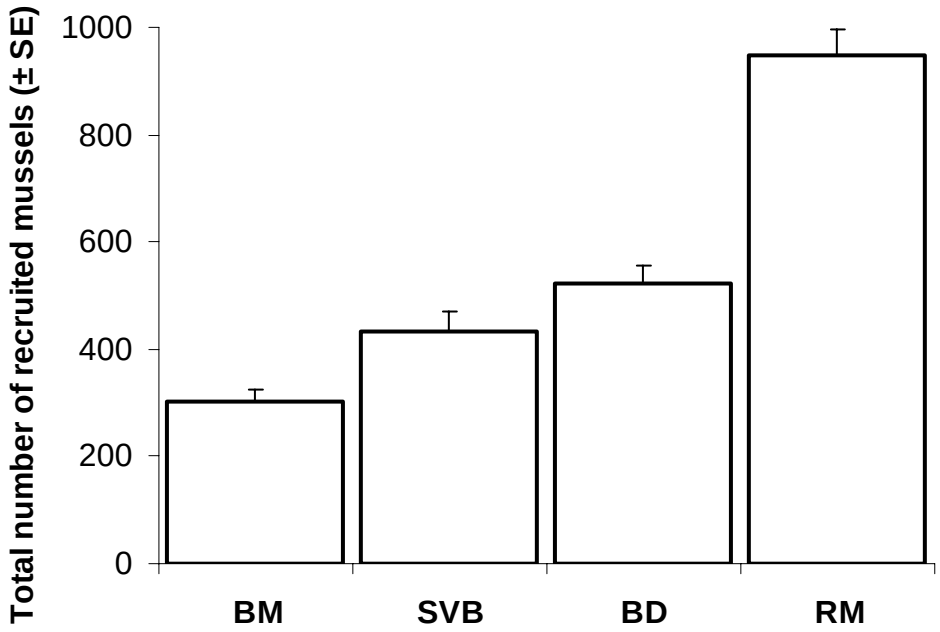

Figure 3.1 Mean total number of mussel species recruiting into five tuffies over 62 weeks at two algal dominated and two mussel dominated sites: Black Miller (A1), Slow Vehicle Bay (A2), Blue Duck (M1), and Raramai (M2) mussel species are: *Mytilus galloprovincialis, Perna canaliculus, Xenostrobus pulex* and *Aulacomya ater maoriana*.

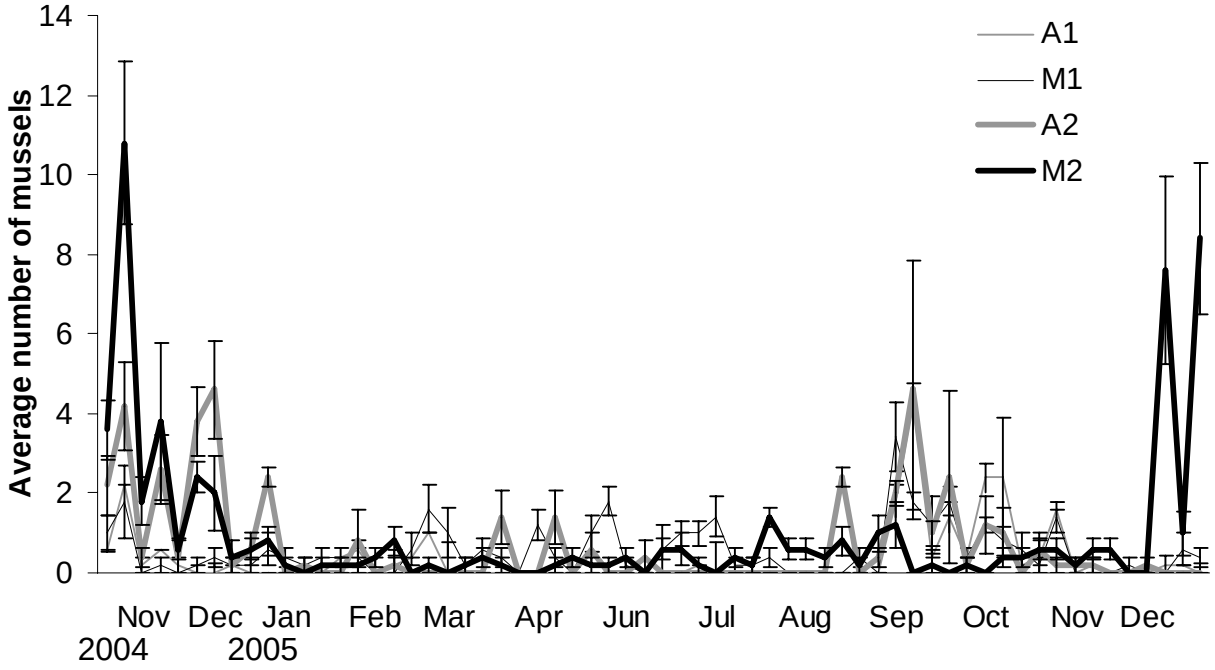

Figure 3.2 The average number of *Mytilus galloprovincialis* recruits (± SE) in five tuffies at each of the four sites: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), and Raramai (M2) for 62 weeks from October 2004 until December 2005.

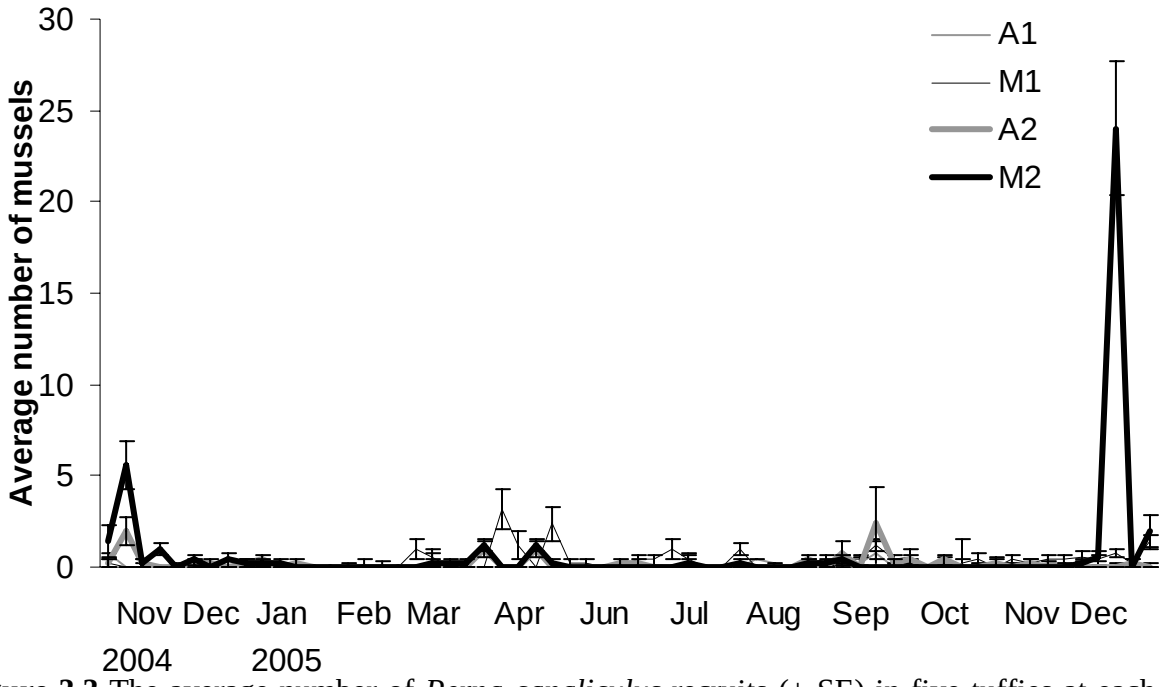

Figure 3.3 The average number of *Perna canaliculus* recruits (± SE) in five tuffies at each of the four sites: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), and Raramai (M2) for 62 weeks from October 2004 to December 2005.

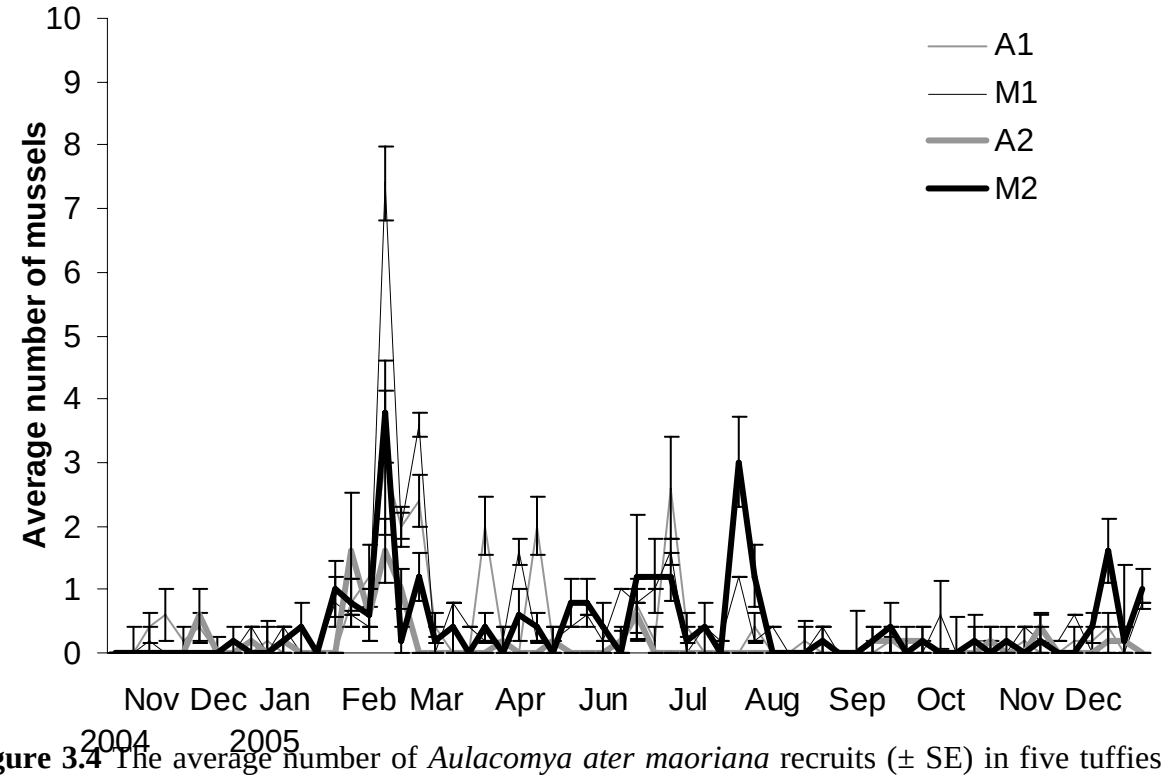

Figure 3.4 The average number of *Aulacomya ater maoriana* recruits (± SE) in five tuffies at each of the four sites: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), and Raramai (M2) for 62 weeks from October 2004 to December 2005.

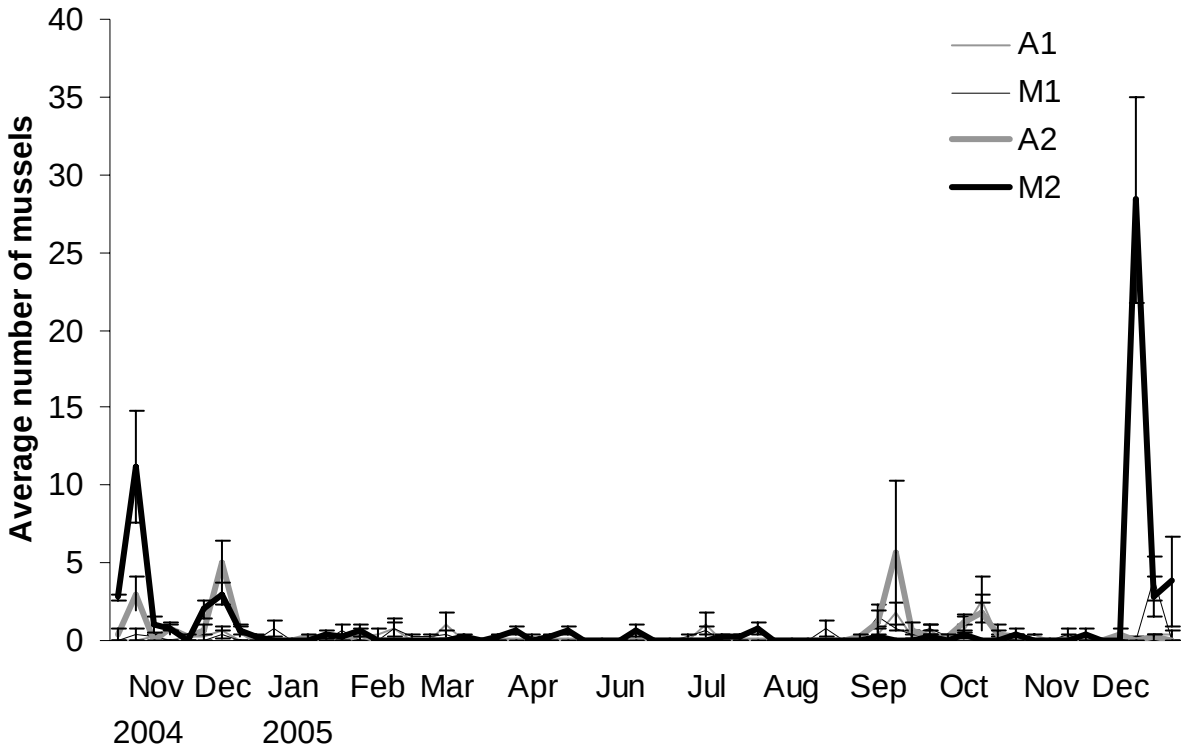

Figure 3.5 The average number of *Xenostrobus pulex* recruits (± SE) in five tuffies at each of the four sites: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), and Raramai (M2) for 62 weeks from October 2004 to December 2005.

All unidentified bivalve larvae/recruits in tuffy samples were pooled. The greatest peak in recruitment was found in March at Black Miller, an algal dominated habitat (Figure 3.6). There was significant variation within sites for bivalve recruitment ($F_{2,1175}$=5.7880, P=0.003) but these unidentified bivalve species did not preferentially settle into habitats dominated by mussels.

The presence of small micro-grazing gastropods may facilitate mussel settlement and subsequent establishment of adult mussel beds by reducing algal cover that otherwise may smother juvenile mussels (Underwood 1981). A nested ANOVA of mean recruited gastropods, showed that recruitment between sites was significantly different ($F_{2,62}$ = 3.216, P=0.042) . Gastropod recruitment was greatest in March, peaking at the same time as unidentified bivalves (Figure 3.7). However, differences between habitats were not significant as there was a large amount of variation within algal habitats.

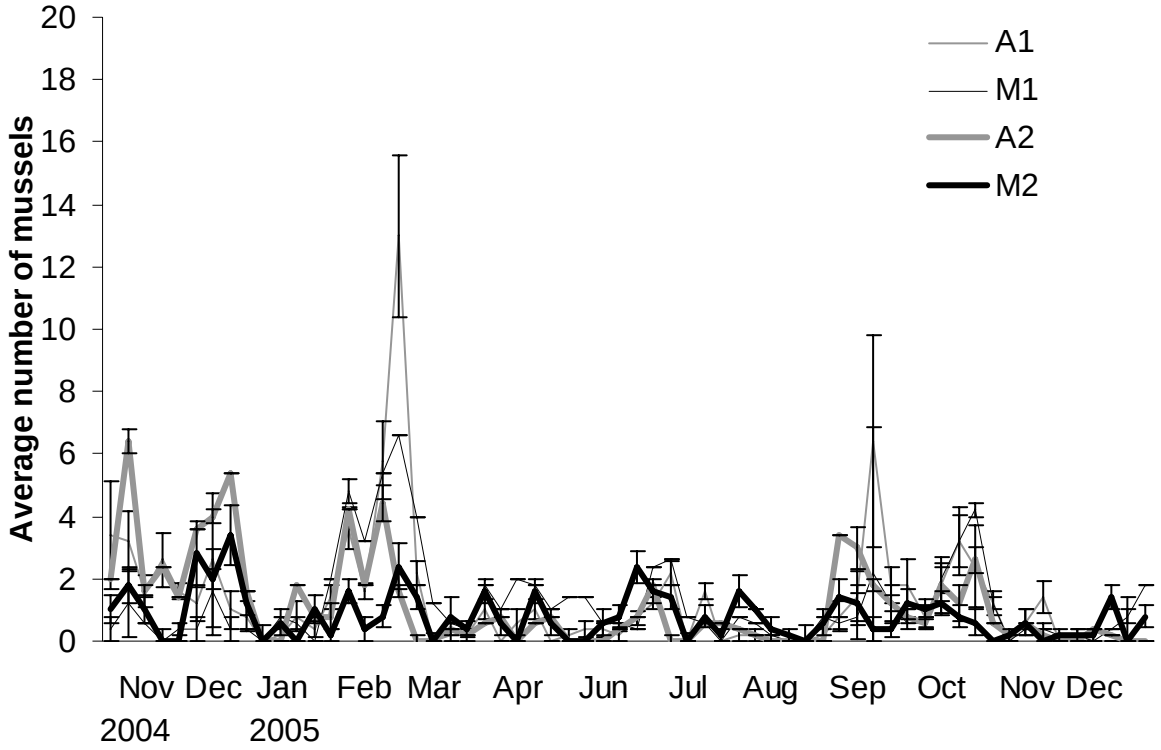

Figure 3.6 The average number of unidentified bivalve larvae (± SE) in five tuffies at each of the four sites: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), and Raramai (M2) for 62 weeks from October 2004 until December 2005.

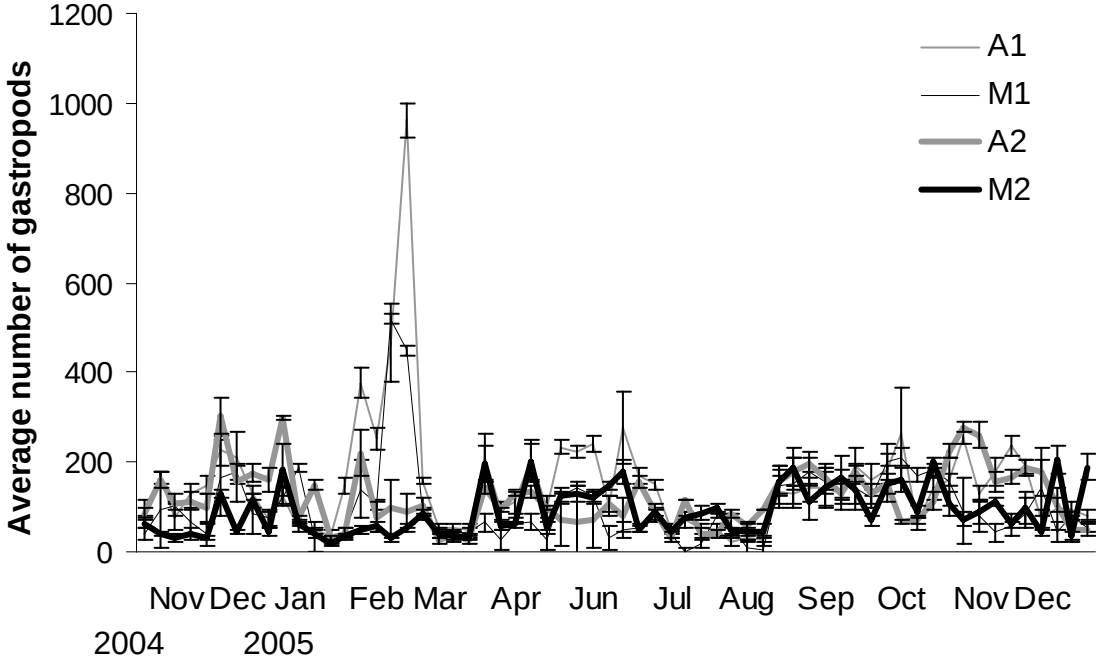

Figure 3.7 The average number of gastropod larvae (± SE) in tuffies at each of the four sites: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), and Raramai (M2) for 62 weeks from October 2004 until the end of December 2006.

3.3.2 Mussel bed core samples

The low shore mussel beds at Blue Duck and Raramai were composed of 3 mussel species, *Perna canaliculus, Mytilus galloprovincialis* and *Aulacomya ater maoriana.* The most abundant mussels at Blue Duck were large adult *P.canaliculus* (40-90mm), while Raramai was mainly composed of *M.galloprovincialis* (31-40mm). These differences in mussel bed composition resulted in the significant 'site' x 'size class' interaction for both species (Table 3.3). *A.ater maoriana* was found at both sites in similar numbers. However, there were significant differences in size between sites and times, because *A.ater maoriana* recruits were more abundant at Blue Duck and Raramai (Figures 3.8 and 3.9). Early recruit-sized *P.canaliculus* (<10mm) and *M.galloprovincialis* (<10mm) were found in samples throughout the year and their number did not differ greatly between sites (Figure 3.9). This is in contrast to the recruitment numbers found with the tuffy sampling.

These core samples are a cumulative sample. Small mussels do not appear to be moving through the size classes. All large mussels are *P. canaliculus*, while most middle-sized mussels are *M. galloprovincialis* at Raramai, but not at Blue Duck. The smallest size-class reflects overall order of recruit abundance in tuffies. There seems to be considerable post-recruit sorting of abundances among species.

For *P.canaliculus* and *M.galloprovincialis* the abundance within size classes was significantly different between months, but also varied between sites (Table 3.3) This was not true of *A.ater maoriana.* The significant 'site' x 'size class' interaction for *A.ater maoriana* was due to an increase in the number of larger sized *A.ater maoriana* found at Raramai. The significant 'month' x 'size class' interaction term for *A.ater maoriana* was due to the presence of larger size classes in some months, but not others.

Table 3.3 Factorial ANOVA for core samples on the effect of site (n=2), month (n=7), and size class (n=9) on the mussel composition of A) *Perna canaliculus*, B) *Mytilus galloprovincialis*, and C) *Aulacomya ater maoriana* at the mussel dominated habitats; Blue Duck (M1) and Raramai (M2). Site and month were treated as random factors.

A) *Perna canaliculus*

Source of variance	**df**	**MS**	**F**
Site (S)	1	100.584	2.394
Month (M)	6	7.185	1.876
Size class (SC)	8	55.958	1.285
S x M	6	2.495	0.928
S x SC	8	42.202	**15.700**
M x SC	4	84.023	1.496
S x M x SC	4	82.688	**2.384**
Error	1134	1.127	

*denotes significant result

B) *Mytilus galloprovincialis*

Source of variance	**df**	**MS**	**F**
Site (S)	1	184.137	2.551
Month (M)	6	1.888	0.794
Size class (SC)	8	141.640	1.955
S x M	6	2.257	0.937
S x SC	8	72.341	**30.039**
M x SC	48	2.527	1.049
S x M x SC	48	2.408	**1.920**
Error	1134	1.254	

*denotes significant result

C) *Aulacomya ater maoriana*

Source of variance	**df**	**MS**	**F**
Site (S)	1	16.687	3.500
Month (M)	6	0.125	0.015
Size class (SC)	8	271.455	**20.934**
S x M	6	0.210	1.004
S x SC	8	4.767	**22.733**
M x SC	48	8.410	**40.108**
S x M x SC	48	0.210	0.379
Error	1134	0.554	

Bold = significant result

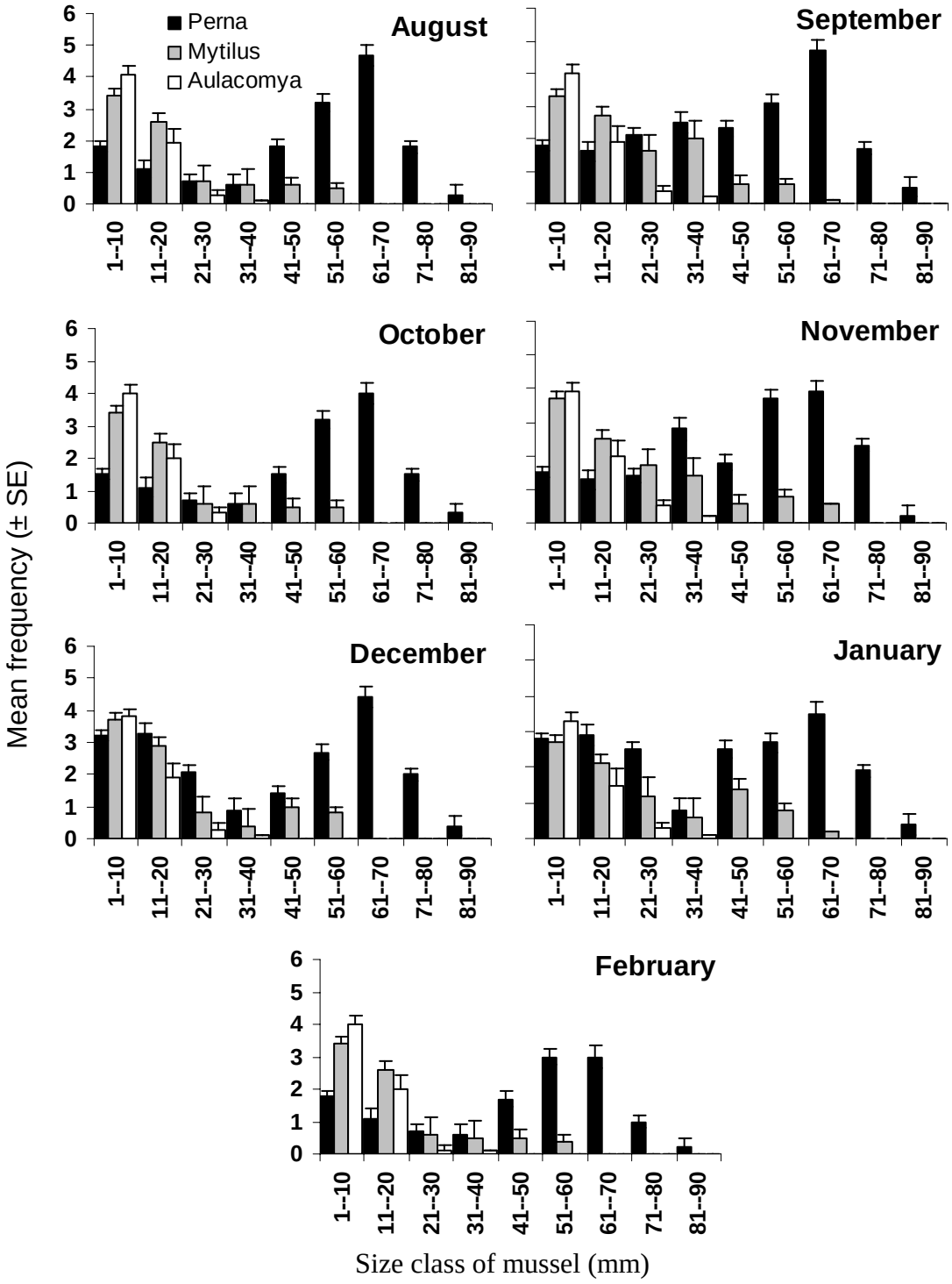

Figure 3.8 Average monthly size frequency data for three species (*Perna canaliculus, Mytilus galloprovincialis* and *Aulacomya ater maoriana*) from ten 10 x 10cm cores from the low shore mussel bed at Blue Duck (M1): Aug 2005 – February 2006.

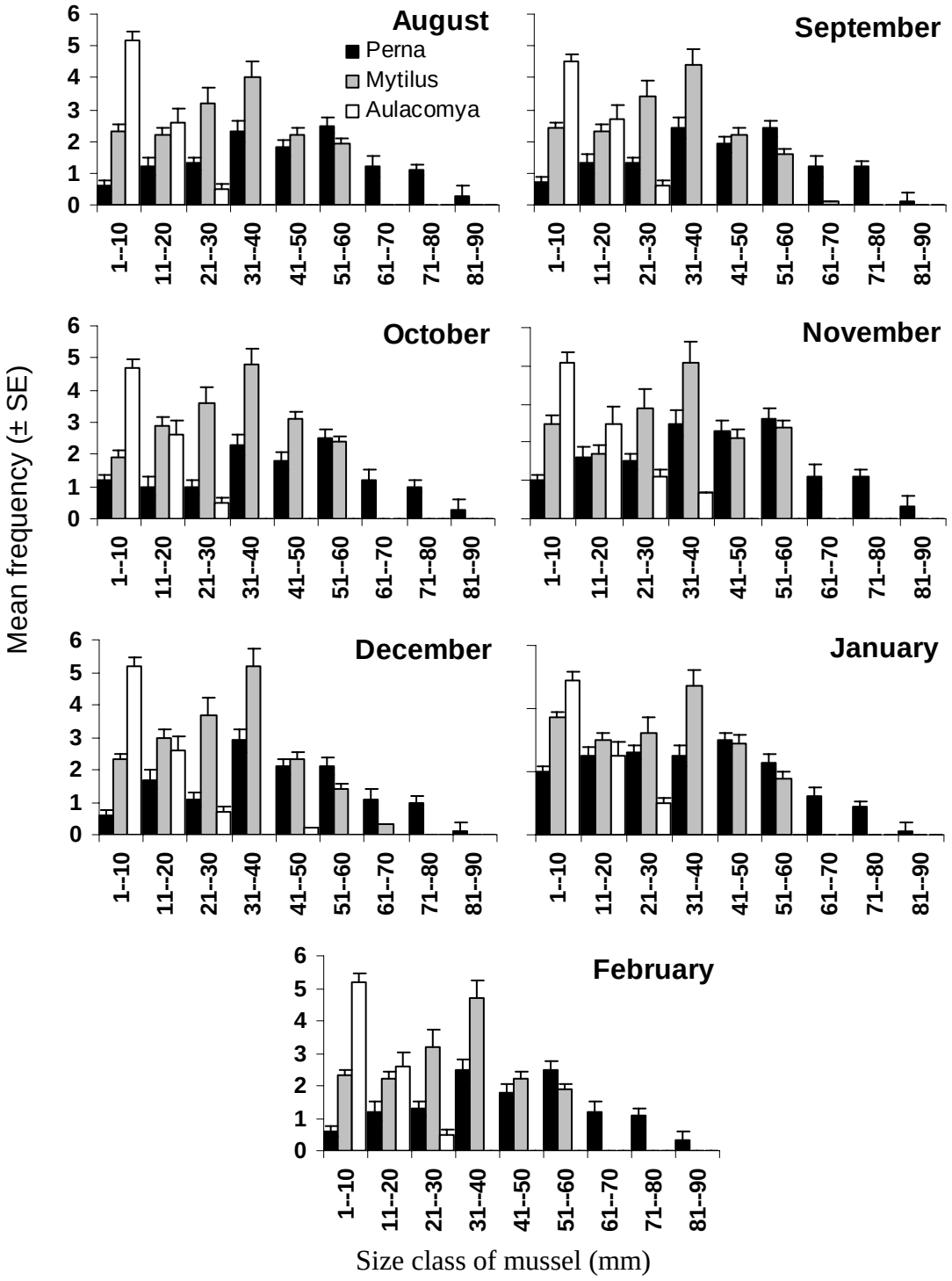

Figure 3.9 Average monthly size frequency data for three species (*Perna canaliculus, Mytilus galloprovincialis* and *Aulacomya ater maoriana*); data from ten 10 x 10cm cores from the low shore mussel bed at Raramai (M2): Aug 2005 – February 2006.

Tuffies are thought to provide an estimate of the numbers of mussels recruiting into natural mussel beds (Figure 3.9). A comparison of recruitment into tuffies and recruitment into surrounding mussel beds appears to confirm this. Small peaks in recruitment of *P.canaliculus* were seen in tuffies in December. The following month (January) another small increase in mussels was seen in cores (Figure 3.9). Possible fluctuations of recruitment into tuffies appeared to be mirrored in subsequent areas in natural mussel beds. This pattern was repeated for *M.galloprovincialis* in December (Figure 3.9). There was a small increase in the number of mussels found in monthly averages of tuffies and this was reflected in the mussel bed one month later. Significant three-way interactions between site, month and collector were found for *P.canaliculus* and *M.galloprovincialis* but not for *A.ater maoriana* (Table 3.4). This interaction suggests that there is a link between recruitment into tuffies and subsequent successful settlement into adult mussel beds.

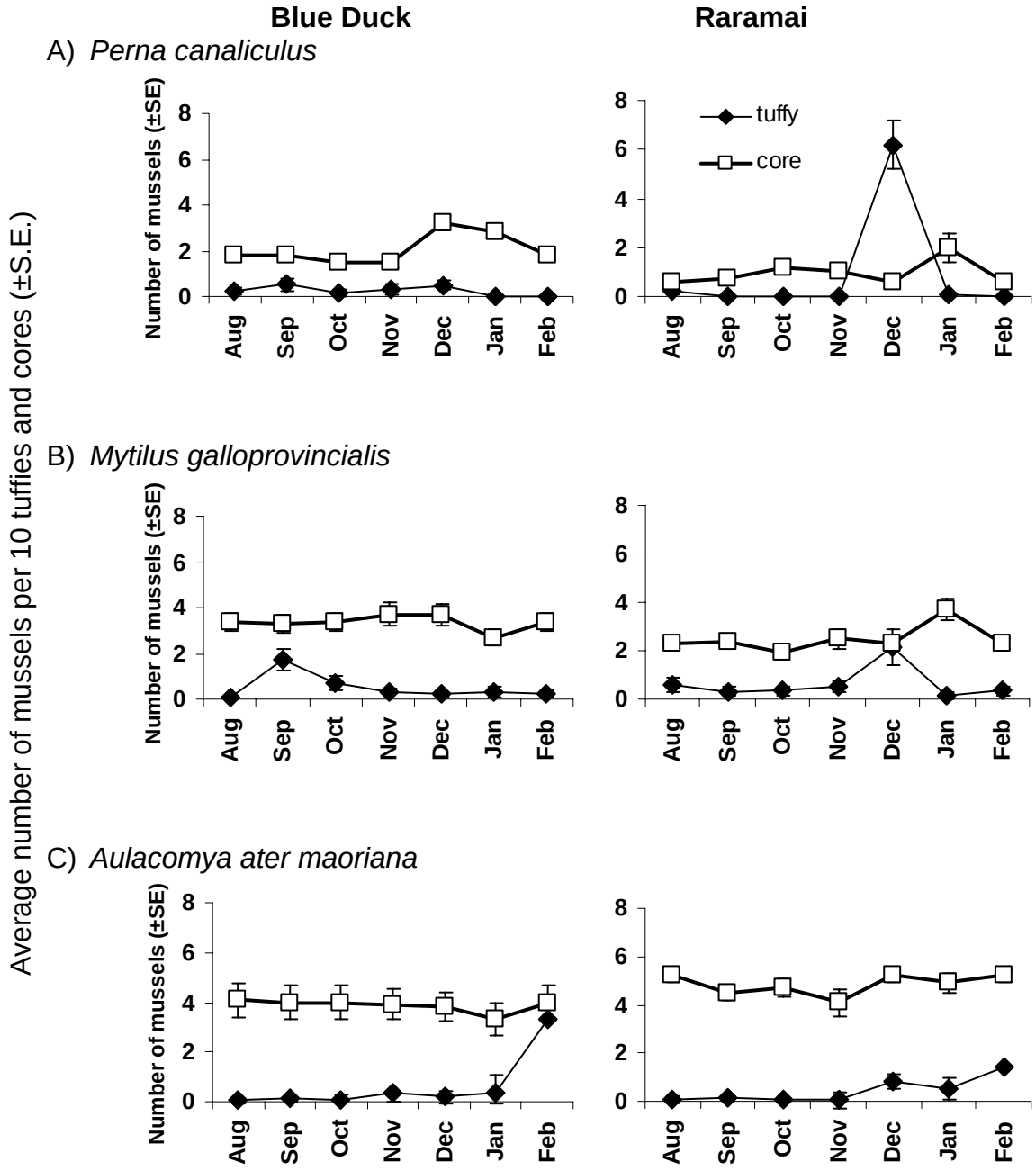

Figure 3.10 Average numbers of recruit-sized mussels in 10 tuffies and cores: A) *Perna canaliculus* (<10mm), B) *Mytilus galloprovincialis* (<10mm), and C) *Aulacomya ater maoriana*(<10mm), in tuffies and cores at Blue Duck and Raramai from August 2005–February 2006.

Table 3.4 Factorial ANOVA of the effects of site (S), month (M), and collector (tuffies vs. cores) (C) on the number of mussel recruits of: A) *Mytilus galloprovincialis*, B) *Perna canaliculus*, and C) *Aulacomya ater maoriana* to tuffies and cores at all sites from December – February 2006.

A) *Mytilus galloprovincialis*

Source of variance	df	MS	F
Site (S)	1	4.629	0.199
Month (M)	6	7.331	2.068
Collector (C)	1	330.057	14.051
S x M	6	7.7119	0.640
S x C	1	27.657	2.294
M x C	6	7.891	0.654
S x M x C	6	12.057	**6.740**
Error	252	1.789	

B) *Perna canaliculus*

Source of variance	df	MS	F
Site (S)	1	3.657	0.036
Month (M)	6	59.073	3.642
Collector (C)	1	20.629	0.189
S x M	6	38.549	0.570
S x C	1	131.657	1.948
M x C	6	45.254	0.670
S x M x C	6	67.582	**9.405**
Error	252	7.186	

C) *Aulacomya ater maoriana*

Source of variance	df	MS	F
Site (S)	1	17.500	1.279
Month (M)	6	1.670	0.964
Collector (C)	1	1168.514	87.545
S x M	6	1.242	2.989
S x C	1	12.857	**30.946**
M x C	6	0.906	2.181
S x M x C	6	0.415	0.261
Error	252	1.590	

Bold= significant result

Experimental carpet plates were placed in cages in the low shore at all sites to examine algal and mussel recruitment. Algal species that were not found in community quadrats recruited onto plates (Figure 3.0, Figure 2.3 and Figure 2.4). Many of these were small branching filamentous algae. Mussels settled onto these plates at all sites in December in relatively large numbers compared to those in tuffy samples (Figure 3.2). Mussel recruitment on carpet plates was not significantly different between algal and mussel habitats in December ($F_{2,22}$=0.320, P=0.577), January 2006 ($F_{2,22}$=0.550, P=0.466) or February ($F_{2,22}$=2.809, P=0.108).

An ANOVA comparing habitats and collectors showed that carpet plates collected a larger number of recruit mussels than tuffies but this varied between habitats (Table 3.5). Despite the possible variation between the surface area of a plate and tuffy, a greater number of mussels were found on carpet plates in both December and January (Figure 3.11, Table 3.5).

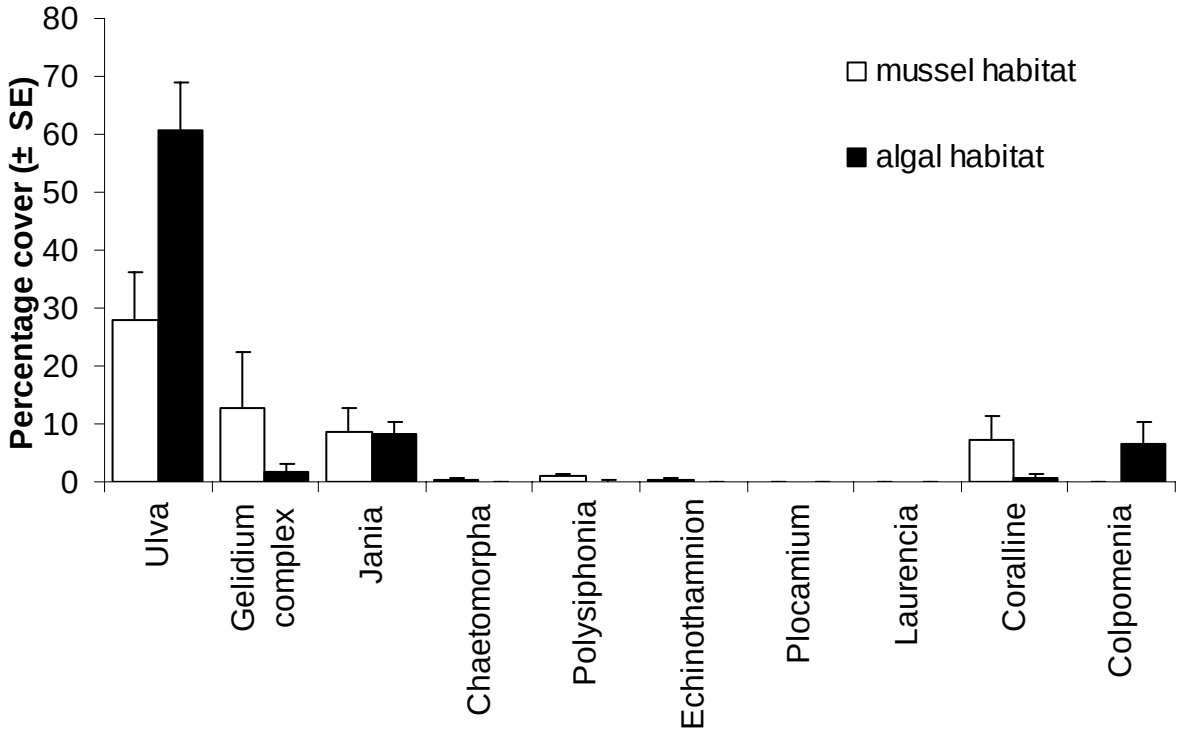

Figure 3.11 Mean percentage cover of algae in cage experiments at mussel and algal dominated habitats in summer 2006. Species are: *Ulva* spp, *Gelidium*/ *Ceramium* complex, *Jania microarthroida, Chaetomorpha coliformis, Polysiphonia* sp, *Echinothamnium* sp, *Plocamium microcladiodes, Laurencia thyrsifera, Corallina officinalis, Colpomenia* sp.

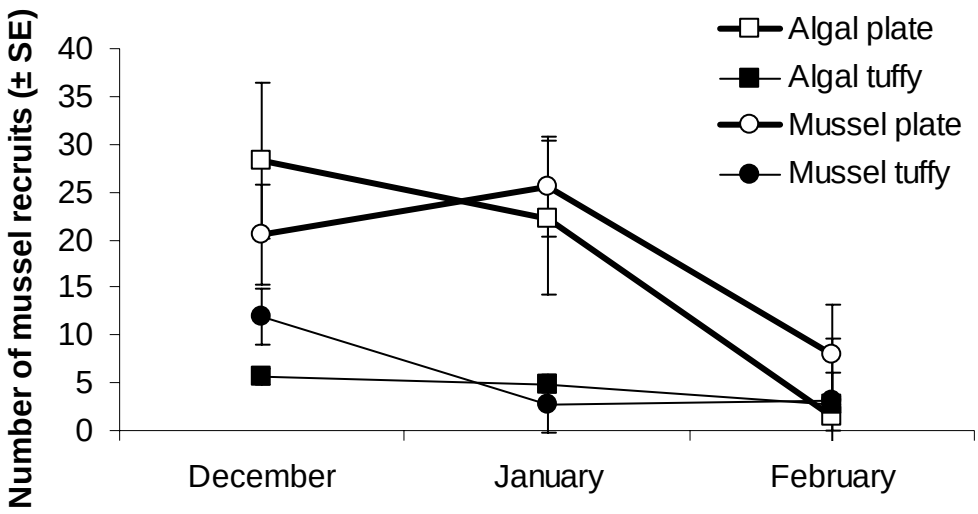

Figure 3.12 Average number of juvenile mussel recruits (± SE) in five tuffies and three plates on the low shore at mussel and algal dominated habitats from December to February.

Table 3.5 Factorial ANOVA on the differences between collectors (carpet plate vs. tuffy) and habitat, on the recruitment of pooled species of mussels in December 2006.

Source of variance	December		January		February	
	MS	F	MS	F	MS	F
Habitat	26.042	0.583	9.375	1.008	96.000	4.097
Collector	876.042	**19.609**	187.042	**20.094**	112.667	**4.808**
Habitat x Collector	22.042	0.493	2.042	0.219	170.667	**7.283**
Error	44.675		9.309		23.433	

Bold= significant result

3.4 Discussion

One hypothesis explaining the absence of mussels from algal dominated intertidal shores is that mussel larvae do not arrive in sufficient numbers to establish populations (Connolly and Roughgarden 1999). In this study, however, I found no significant difference between mussel and algal dominated habitats in the number of recruiting mussels. Recruit-sized mussels were found in small numbers throughout the year in core samples from mussel dominated habitats. However, recruitment, as measured by tuffies and carpet plates, was extremely low in both algal and mussel habitats. The intensity of recruitment into an intertidal habitat is thought to be the main determinant of the types of species that will dominate an assemblage and resulting strength of the post-recruitment processes that affect community composition (Gaines and Roughgarden 1985, Gaines and Bertness 1992, Connolly and Roughgarden 1999). However, I found two types of assemblages occur where there are equal rates of mussel recruitment. Consequently the strength of recruitment intensity in these locations is thought to be less important and post-recruitment processes are considered more likely to influence the community composition in these locations.

My tuffy study found no significant difference in recruitment into mussel versus algal habitats. Adult mussel beds are known to provide a suitable habitat for mussel settlement, and experiments with various substrata have indicated that mussel larvae have a preference for firm roughened surfaces that have a discontinuous texture (Seed and Suchanck 1992). However, the direct settlement of juvenile mussels into adult mussel beds has been a controversial topic. Bayne (1964) found evidence of *Mytilus edulis* settling onto filamentous algae, and then migrating to adult mussel beds after a period of growth (secondary settlement). Several studies have supported the concept of secondary settlement (Paine 1974, Seed and Suchanck 1992, Buchanan and Babcock 1997), but others have rejected the idea. For example, the number of mussels settling into both filamentous algae and mussel clumps on South African shores was not significantly different suggesting an absence of secondary settlement (McQuaid and Lindsay 2005). However, Paine (1974) examined the various substrata that *Mytilus*

californianus recruited to in Mukkaw Bay, Washington State. He found that *M. californianus* preferentially settled amongst the filamentous red alga *Endocladia municata* in the mid intertidal and then underwent secondary settlement, migrating towards more suitable mussel habitats. However, in low shore quadrat data taken from Kaikoura no filamentous branching algae were present except for turfing corallines and thus I found no evidence of recruitment into them. However, greater numbers of mussels settled onto the dense, damp matrix provided by carpet plates

Regardless of the presence of primary or secondary settlement, small differences were found in seasonal recruitment patterns between species. *P. canaliculus* rarely featured in tuffy samples and *A. ater maoriana* recruitment was greatest during the late winter months (July-August). This is consistent with observations made by Kennedy (1977) who found that spawning of *A. ater maoriana* began in August. *M. galloprovincialis* was the most abundant mussel species in all plate and tuffy samples in my study and was also the most abundant species at east coast sites in another study of mussel recruitment (Menge et al. 1999). *M. galloprovincialis'* presence in collectors also followed seasonal patterns. These patterns in mussel recruitment are thought to be linked with sea temperature because temperature is known to affect mussel reproduction (Kennedy 1977).

Sea temperature is a principal environmental factor that can directly affect the reproductive output of mussels (Kennedy 1977). Mussels of the genus *Mytilus* are widely distributed in cooler waters in both the northern and southern hemispheres. Maturation of gametes generally occurs as seawater temperatures drop over winter months and spawning is initiated as seawater temperature increases in spring (Kennedy 1977). However, some species of mussels do not rest, and produce gametes all year round. This appears to be the case with the mussel populations in Kaikoura. *M. galloprovincialis* showed an increase in recruitment starting in October, just after the warmer temperatures of spring began (Figure 3.2). However, recruitment did occur all year round in all mussel species. Studies in South Africa, looking at the effects of temperature and exposure in determining community composition, have suggested that temperature induces a framework of species composition on different beaches.

However, exposure influences the biomass of many of the species which dominate these shores (McQuaid and Branch 1984). Sea temperature data collected from Kaikoura during the study period suggest that it was not an unusual year for water temperatures (Figure 2.2). There were no fluctuations in sea temperature near the Kaikoura Peninsula and therefore, no evidence of any upwelling episodes (Figure 2.2).

A large number of other bivalve species were present in tuffy samples; while these bivalves were unidentified their presence shows that a significant larval pool may exist in nearshore waters. The supply of propagules is thought to have significant effects on populations and community structure and the intensity of recruitment can be the driving force behind post-recruitment processes (Menge et al. 1999, Connolly et al. 2001, Shanks and Brink 2005). In California and Oregon, upwelling currents are thought to cause offshore flow, and the movement of propagules away from suitable settlement sites, thereby reducing the concentrations of larvae to benthic communities and settlement is thought to only occur during upwelling relaxation (Connolly et al. 2001). Kaikoura is geographically unique as along-shore advection and upwelling episodes combine to limit the cooling effects normally found with upwelling events (Chiswell and Schiel 2001). One possible consequence of reduced upwelling episodes may be a lack of onshore transport upon which mussel larvae rely upon to return to shore. There are several factors that determine the distribution of propagules following dispersal. These include the density and distribution of reproductive adults, the timing and magnitude of their reproductive output and the probability distribution of juvenile transport distances after release from an adult (Gaines and Bertness 1993). Rilov and Schiel (2006) showed that the numbers of settling mussels on the east coast can be orders of magnitude greater than tuffy samples taken from Kaikoura have shown. They suggested that sites without subtidal reefs which had less predation pressure had a greater settlement rate of mussels. As all sites used in this study had extensive subtidal reefs, recruitment limitation in Kaikoura is likely to be a combination of limited upwelling episodes on the east coast and the negative feedback mechanisms associated with few source populations. Only small adult populations are found along the Kaikoura coast, resulting in a meagre output of larvae and, therefore, low concentrations of recruits that are successfully returning to the shore. However, mussels on the east

coast have found ways to successfully establish themselves on some rocky shores despite these major oceanographic hurdles.

Several localised factors are known to interfere with the ideal conditions for growth and reproduction in mussel species including wave exposure (Steffani and Branch 2003), temperature (Kennedy 1977), food availability (Dahlhoff and Menge 1996), parasites (Calvo-Ugarteburu and McQuaid 1998) and epiphytes (Dittman and Robles 1991). Epiphytes interfere with internal temperature regulation and evaporative cooling. They may also reduce food availability by screening out food particles. Suchanek (1981) demonstrated that herbivores associated with the mussel bed (i.e. limpets, chitons and grapsid crabs) keep the mussels free of facultative epiphytes or clear free living algae from rock surfaces. However, algal species have also been shown to enhance mussel settlement by providing suitable substrata. I found the recruitment of algae and mussels was enhanced on carpet plates when compared to the surrounding substrata. Interestingly the species of algae on plates were not generally found in low shore algal assemblages. A greater abundance of finer branching red algal species (*Gelidium*/ *Ceramium* complex, *Jania microarthroida, Chaetomorpha coliformis, Polysiphonia* sp, *Echinothamnium* sp, *Plocamium microcladiodes, Laurencia thyrsifera, Corallina officinalis, Colpomenia* sp) and leafy *Ulva* were present (Figure 3.11) and a comparatively large number of mussels recruited to the algal covered carpet plates (Figure 3.12). Mussels have been shown to preferentially settle into filamentous substrata and combined with the ameliorative effects of shading; the algal canopy on these plates may have provided a more suitable habitat and facilitated mussel recruitment.

Algal canopies are generally thought to have negative effects on algal recruitment. In the Gulf of Maine *Modiolus* mussels overgrown by upright algae are often dislodged because the algae increase the hydrodynamic drag forces on the mussel (Witman 1987). In my study the algal canopies at all sites were dominated by the bull kelp *D. antarctica*. Raramai also had an average cover of 25% of *C. maschalocarpum.* Generally, the relative abundances of common species on various shores may be used as a biological scale for wave exposure. *D. antarctica* is the largest fucalean species

and the whiplash effects from its fronds, which can reach lengths of 10m, can hinder other algae from residing in the same habitat (Taylor and Schiel 2005). *D. antarctica* was also present amongst the low shore mussel species and juvenile *D. antarctica* recruited to the bare rock around the mussel beds as well as onto the shells of adult mussels. Paine (1971) also suggested that it was possible in areas of heavy surf action, that the thick algal blades abrade loosely attached organisms like *P. canaliculus,* or inhibit larval recruitment or settlement. However, this does not seem to be the case at Blue Duck, where *D. antarctica* is interspersed amongst the low shore mussel bed. The cover of turfing corallines was consistently high at algal and mussel sites in Kaikoura. Turfing species can have positive and negative effects on mussel growth and survival because they screen food, limit light and increase temperature, but also provide a filamentous substrate suitable for mussel settlement (Dittman and Robles 1991). However, I found no evidence of mussels recruiting into coralline turfs at any site.

Rates of recruitment are thought to be the main determinant of the adult densities and post-recruitment processes on rocky intertidal shores (Connolly and Roughgarden 1999). However, in my study the recruitment of mussels to algal and mussel dominated habitats was not significantly different and was consistently low year round. The recruitment of mussels to carpet plates was higher than that found in tuffies. The ameliorative affects of algae and reduced levels of grazing appeared to enhance the suitability of the plates facilitating mussel recruitment. However, mussel numbers on plates were similar at mussel and algal dominated habitats suggesting that recruitment rates may not be the main determinants of adult densities on the rocky intertidal shores of Kaikoura.

Introduction

Mussels are primary space occupiers that can outcompete other sessile invertebrates (Seed and Suchanck 1992) and algae (Paine 1966, Dayton 1971, Paine 1971, Menge 1976). However, reasons for their absence from many shores that provide seemingly suitable physical and environmental conditions remain unknown. Several processes may explain their distribution including recruitment intensity (Connolly and Roughgarden 1999, Forde and Raimondi 2004), competition (Keough 1984) and predation (Menge 1976). Kitching et al. (1959) hypothesised that the discontinuous distribution of Mytilus in the Lough Ine area was due to predation and Paine (1974) suggested the lower limits of *Mytilus* beds in New Zealand were the result of *Stichaster* predation. In another study the occurrence of macroalgae, barnacles and mussels in New England depended on the ability of the dogwhelk *Nucella lapillus* to control mussels (Menge 1976, 1978a). In this chapter I test the effects of predation on recruit sized mussels around Kaikoura.

The role of predation in structuring rocky shore communities has been studied extensively worldwide, specifically the roles of predators on dominant taxa such as mussels. However, Schiel (2004) explained the need for a greater emphasis to be placed on earlier life stages of mussels in predation experiments. Many researchers have used mussels in predation experiments that have already reached post-settlement sizes (Petraitis 1998, Menge et al. 1999, Menge et al. 2003, Garza 2005). He suggested that making presumptions about predation intensity on mussels that have seemingly already reached a size where they are no longer susceptible to predation by most predators, would not allow a sufficient understanding of top-down interactions in this system. The amount of time between settlement and recruitment to natural mussel beds is often significant and the effects predators have on these stages of mussels may give insight into the actual interaction strength associated with different oceanographic regimes and the importance of top-down interactions. For example, Rilov and Schiel (2006) found that predation by crabs and fish was so intense o mussels <1cm long, that large recruits were rarely seen at some sites.

To achieve an understanding of the how predation affects the earlier life stages of mussels and, therefore, how top-down systems interact with community structure, Schiel (Schiel 2004) suggested using reciprocal transplant experiments to clarify the roles and capabilities of these dominant taxa. Sites around Kaikoura Peninsula provide an excellent testing ground for these types of hypotheses, as areas with seemingly similar physical conditions are dominated by two types of habitat assemblages in the low-shore zones: by either algae or mussels. One hypothesis is that algal habitats are thought to occur where predation intensity on mussels is too great for populations to become established.

In conjunction with predation experiments, the examination of mussel growth in algal and mussel habitats will allow a greater insight into other mechanisms that may affect mussel distribution. If the two main influences on community patterns, recruitment and predation, are removed growth rate patterns may give an indication of other important aspects that promote the survival, growth and eventual dominance of mussels in a habitat (Petraitis 1995, Alunno-Bruscia et al. 2000, Gardner 2000, Steffani and Branch 2003).

This chapter examines the survival of mussels transplanted into algal and mussel dominated habitats and tests the effects of predation in the low- and mid-shore. Rates of mussel removal from plates should give an indication of the types of predators that are causing the greatest impact on mussel distribution and if there are differences in predation rates between the two habitats. Mussel growth rates will highlight other factors that may be fundamental to the distribution of mussels on shores around Kaikoura.

4.2 Methods

To determine the effects of predators on survivorship of juvenile mussels at algal and mussel dominated sites, I did three experiments with predator exclusion cages. On the 7th of February 2005 I transplanted plates that have been settled with on average of 47 juvenile *Xenostrobus pulex* (S.D. = 14.91, N= 60 plates). Mussels were taken from Cave Rock on Banks Peninsula where the largest concentrations of small (<10mm) mussels occurred. Mussels were placed onto 10 x 10 cm² carpet plates (plastic plates with nylon loop pile carpet glued (Gorilla glue) to one side) and a central hole drilled. Plates were then covered with nylon shade cloth (green wind stop ultra, permathene) and were transported to the Kaikoura sites and secured with 8mm stainless steel screws to the low intertidal for 4 weeks to allow time for byssal threads to attach firmly and to prevent predation while mussels were attaching.

At each site, five replicates of each of three treatments, open plots (plate with no cage), control cages (mesh top and two sides covered) and full cages (mesh on all sides and top), were established on the low shore resulting in a total of 15 plots at each of the four sites. Benthic species were cleared to allow the cages to be attached firmly. Large algal fronds in the vicinity of the treatments were also removed to prevent tangling and whiplash. The cages were made of 6-mm steel rods welded together to form a 20 x 20 x 20 cm cube. Cages were covered in rigid plastic mesh with holes 16 x 16mm that was secured to the cages with cable ties. This mesh and cage design excluded all intertidal predators larger than 16mm. Once the juvenile mussels had attached firmly to the carpet plates the shade cloth was removed and the plates were placed randomly into treatments. Once the plates were placed in their correct treatments the total number of mussels on the plate was counted and recorded. Each plate was numbered allowing the number of mussels surviving on each plate through time to be measured. To eliminate effects of different start times, experiments were started and counts of mussel were done at all sites on the same day. Because of rapid predation, plates were counted every day for the first 5 days and then at increasing intervals for the length of the experiment.

In August 2005 the original predator exclusion experiment was repeated with *Xenostrobus pulex.* All conditions remained the same except a larger number of mussels were used on each plate (Mean = 56 S.D. = 8.65, N= 60 plates). Growth was also examined in this experiment and was measured by taking 25 replicate lengths (distance from anterior to posterior edge in mm) with callipers, of random mussels on caged plates at each site. Counts and measurements were performed for a period of 210 days (7.5 months) to examine differences in growth rates at different sites.

Xenostrobus pulex is generally found in the mid to high shore at the two mussel sites used in this series of experiments. Therefore, to test rates of predation at a higher shore level, cages were attached in the mid- tidal zone at all sites. Experimental plates and cages were made in the same manner as before and the same predator exclusion experiment was repeated in the Mid-shore in December 2005.

Stichaster australis were counted during 5 replicate low tide periods at each site by visually surveying around the edge of the site to establish if the abundance of this predator was correlated with the presence of mussel beds.

Standard analyses of survivorship data over time usually involve the use of repeated measures ANOVA. However, the main assumption of repeated measures is that data are normally distributed over time. Survivorship data in my study were not normally distributed and were often right skewed. Consequently nested ANOVA's were done on arcsine-square-root percentage survival data for each day. In the ANOVA models the differences between habitats (algal, mussel), sites (nested within habitat; A1, M1, A2, M2) and treatments (no cage, full cage, control), with regards to survivorship, were calculated for each day a count was performed. Cochran's tests were used to test homogeneity of variances. Tukey's tests were used as a post-hoc analysis to determine differences between treatments.

Plate 4.1 Carpet plates covered with plastic shade cloth to allow mussel byssal attachment.

Plate 4.2 *Stichaster australis*- predatory sea-star near a full cage designed to reduce intertidal predation on transplanted mussels.

4.3 Results

No significant difference in survival of mussels was found between habitats in the first transplant experiment (Table 4.1). The first predation experiment started in March 2005 and continued for 31 days. However, mussel survival differed significantly between treatments at all times (Table 4.1). Significant treatment effects at all times were due to greater percentage survival on caged plates compared with open and control plates (Table 4.1; Tukey HSD, $P < 0.05$). However, on day 31 treatment effects were caused by significant differences between remaining mussels in cages (Figure 4.1; Tukey HSD $P<0.05$) Mussels exposed to predators (no cage) were quickly removed from plates at all sites (Figure 4.1). Ten days after the experiment started, less than 20% of the original mussels remained on open plates (Figure 4.1). By day 31, all mussels on open plates had been removed except at Blue Duck where only 3% of the original mussels remained (Figure 4.1). On days 1 and 3 the mean numbers of mussels surviving at Blue Duck was greater than those found at all other sites (Figure 4.1; Tukey HSD, $P < 0.05$).

Table 4.1 Nested ANOVA (significance: * = 0.05, ** = 0.01, *** = 0.001) of the differences between habitats (algal, mussel), sites (nested within habitats: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), Raramai (M2)), treatments (no cage, full cage, control) and interaction terms on the arcsine-square-root percentage survival numbers for the first low-shore mussel predation experiment for days 1, 9, and 31.

Source of variation		**day 1**		**day 9**		**day 31**	
	df	MS	F	MS	F	MS	F
Treatment (T)	2	1583.4	2.265	3268.9	8.203*	3221.0	13.147**
Habitat (H)	1	1244.3	0.654	617.9	1.835	1193.6	4.565
Site(Habitat) (S(H))	2	1902.7	2.723	366.8	0.845	261.2	1.066
T x H	2	169.2	0.242	124.9	0.313	84.9	0.347
T x (S(H))	4	698.8	4.550**	398.6	4.439**	245.0	2.957*
Error	48	153.6		89.8		82.9	

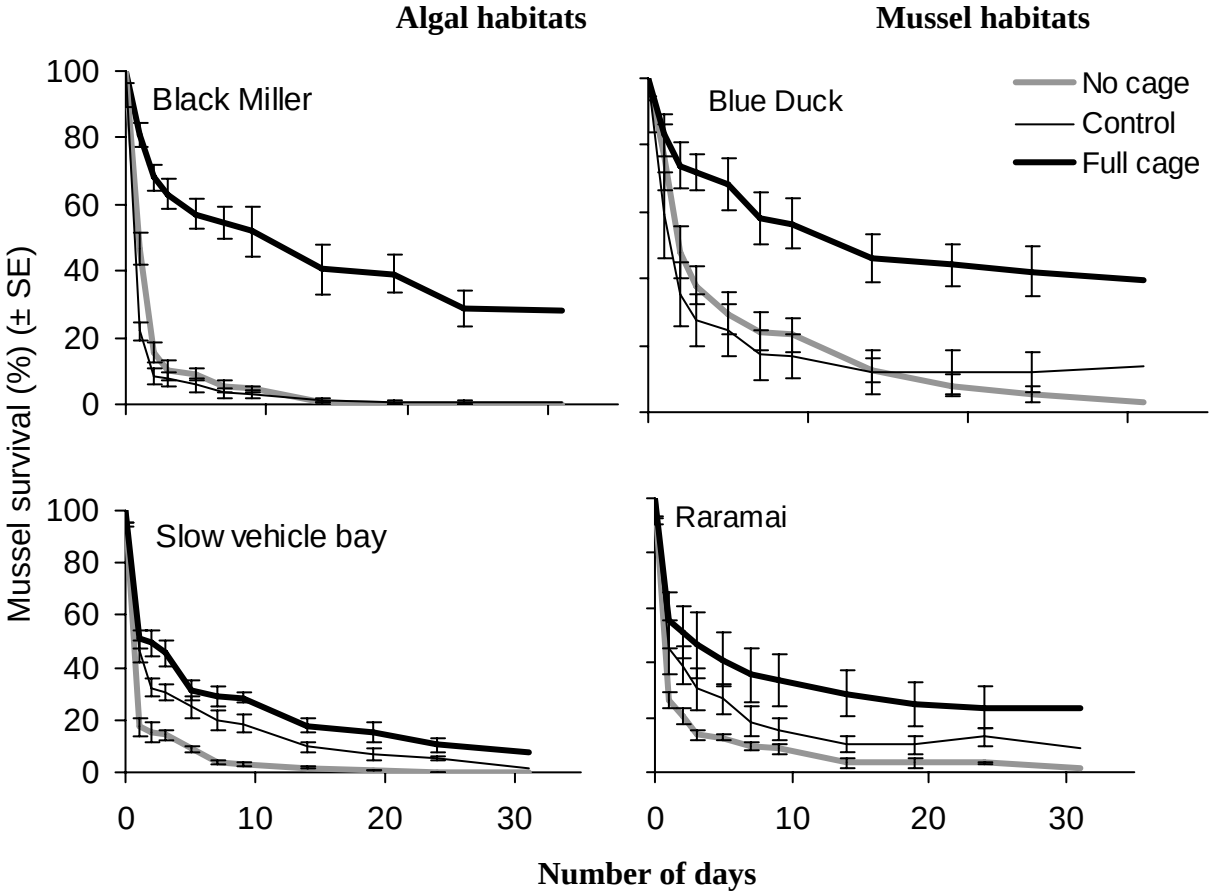

Figure 4.1 *Xenostrobus* first low-shore predation experiment. Percentage survival (mean ±SE) of small mussels (≤ 1cm) exposed to all predators (no cage), exposed to no predators (full cage) and a cage control (control) at sites dominated by algae (Black Miller, Slow Vehicle Bay) and sites dominated by mussels (Blue Duck, Raramai) in march 2005.

The low-shore predation experiment was repeated in August 2005 and ran for 210 days, finishing in March 2006. All conditions were similar except a slightly greater number of mussels on plates were used. Again, mussel survival in algal and mussel dominated habitats was not significantly different until all mussels were removed from algal dominated habitats after 118 days (Table 4.3). Significant differences in survival between treatments were found soon after experiments began (Table 4.2). On days where significant differences were found between treatments, they were found to a result of mean survival on caged plates being significantly greater than that on open and control plates (Figure 4.2; Tukey HSD, $P < 0.05$). No significant differences were found between sites on days 1, 10, 56 and 118 (Tables 4.2 and 4.3). However, site x treatment differences on day 10 were a result of variation between the two mussel

dominated habitats with greater survival being seen in control treatments at Blue Duck (Figure 4.2; Tukey HSD, P< 0.05). This variation between sites and treatments was not seen on day 118 because all mussels had been removed from control treatments (Table 4.3).

Table 4.2 Nested ANOVA (significance: * = 0.05, ** = 0.01, *** = 0.001) of the differences between habitats (algal, mussel), sites (nested within habitats: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), Raramai (M2)), treatments (no cage, full cage, control) and interaction terms on the arcsine-square-root percentage survival numbers for the second low-shore mussel predation experiment for days 1 and 10

Source of variation		**day 1**		**day 10**	
	df	MS	F	MS	F
Treatment (T)	2	10400.0	15.180**	19637.5	20.942**
Habitat (H)	1	4.6	0.002	596.0	0.678
Site(Habitat) (S(H))	2	2022.4	2.952	879.0	0.937
T x H	2	906.4	1.323	299.1	0.319
T x (S(H))	4	685.0	1.738	937.7	3.951**
Error	48	394.1		237.3	

Table 4.3 Nested ANOVA (significance: * = 0.05, ** = 0.01, *** = 0.001) of the differences between habitats (algal, mussel), sites (nested within habitats: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), Raramai (M2)), treatments (no cage, full cage, control) and interaction terms on the arcsine-square-root percentage survival numbers for the second low-shore mussel predation experiment for days 56 and 118.

Source of variation		**day 56**		**day 118**	
	df	MS	F	MS	F
Treatment (T)	2	8237.8	29.808**	6735.0	23.996**
Habitat (H)	1	2.3	2.276	494.7	2.099
Site(Habitat) (S(H))	2	296.1	1.072	235.7	0.840
T x H	2	98.7	0.357	124.2	0.443
T x (S(H))	4	276.4	1.837	280.7	2.153
Error	48	150.4		130.4	

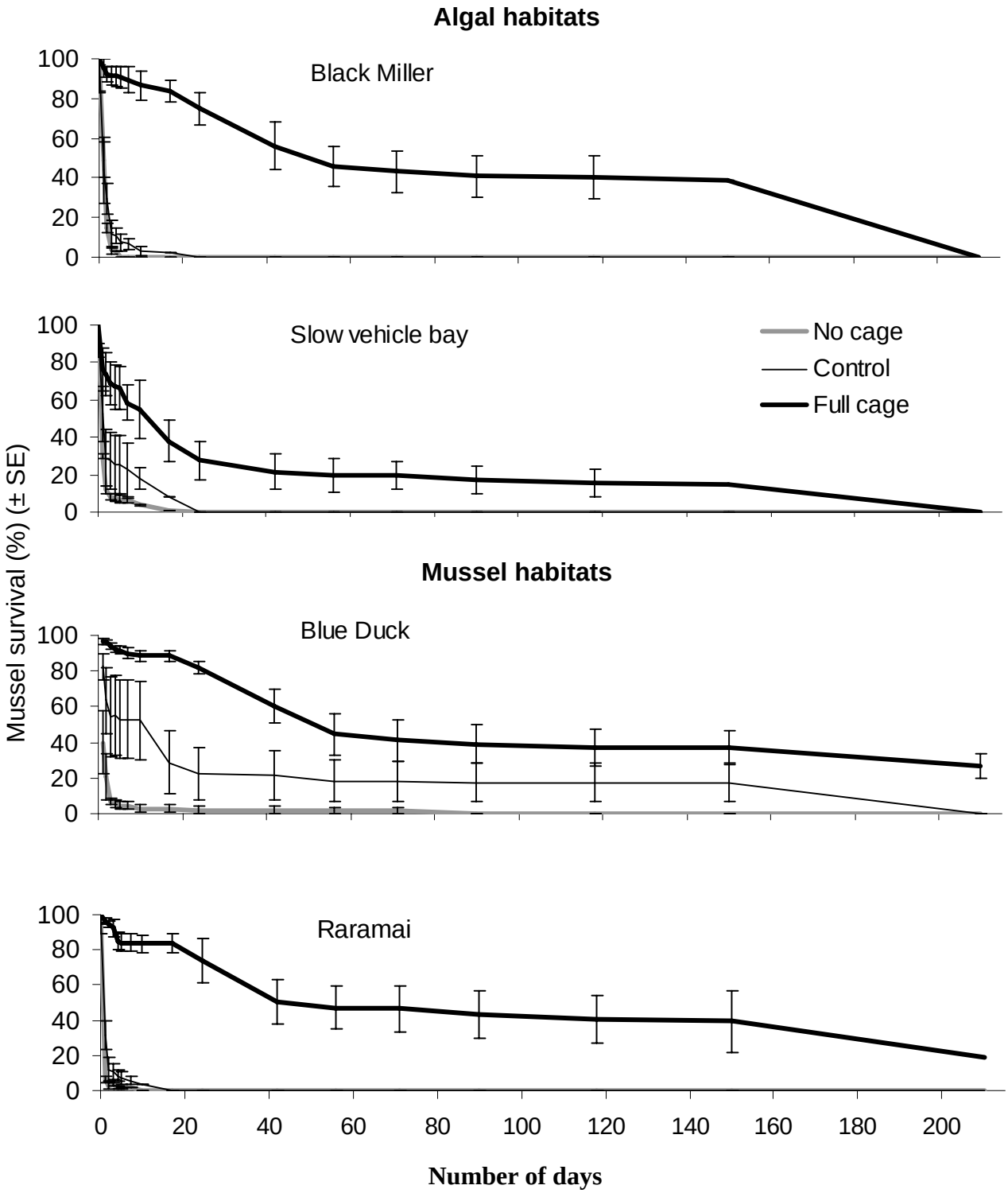

Figure 4.2 *Xenostrobus* second low-shore predation experiment. Percentage survival (mean ±SE) of small mussels (≤ 1cm) exposed to all predators (no cage), exposed to no predators (full cage) and a cage control (control) at sites dominated by algae (Black Miller, Slow Vehicle Bay) and sites dominated by mussels (Blue Duck, Raramai) in August 2005- March 2006.

A predation experiment in the mid-shore began in December 2005 and continued for 76 days (February 2006). No significant difference was found between habitats on day 1, 9, and 76 (Table 4.4; Tukey HSD, P<0.05). In this experiment there were significant differences between treatments (no cage, full cage, control) soon after the beginning of the experiment (Table 4.4). A comparison of means between treatments showed that significant differences between treatments were due to greater survival on caged plates compared with open and control plates (Figure 4.4; Tukey HSD, P< 0.05). Significant differences were found between site x treatment interactions on day 9 and 76 (Table 4.4). This variation was a result of differences found between algal dominated habitats (Tukey HSD, P<0.05). Mussel survival in cages at Slow Vehicle Bay was considerably less than all other sites (Figure 4.3).

Table 4.4 Nested ANOVA (significance: * = 0.05, ** = 0.01, *** = 0.001) of the differences between habitats (algal, mussel), sites (nested within habitats: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), Raramai (M2)), treatments (no cage, full cage, control) and interaction terms on the arcsine-square-root percentage survival numbers for the mid-shore mussel predation experiment for days 1, 9, and 76.

Source of variation		**day 1**		**day 9**		**day 76**	
	df	MS	F	MS	F	MS	F
Treatment (T)	2	739.2	2.026	6768.6	18.372**	15284.8	22.898**
Habitat (H)	1	889.4	2.170	2097.0	9.597	281.9	0.476
Site(Habitat) (S(H))	2	409.9	1.123	218.5	0.593	591.9	0.887
T x H	2	407.2	1.118	178.1	0.483	462.6	0.693
T x (S(H))	4	368.4	1.363	368.4	4.169**	667.5	19.308***
Error	48	207.6		88.4		34.6	

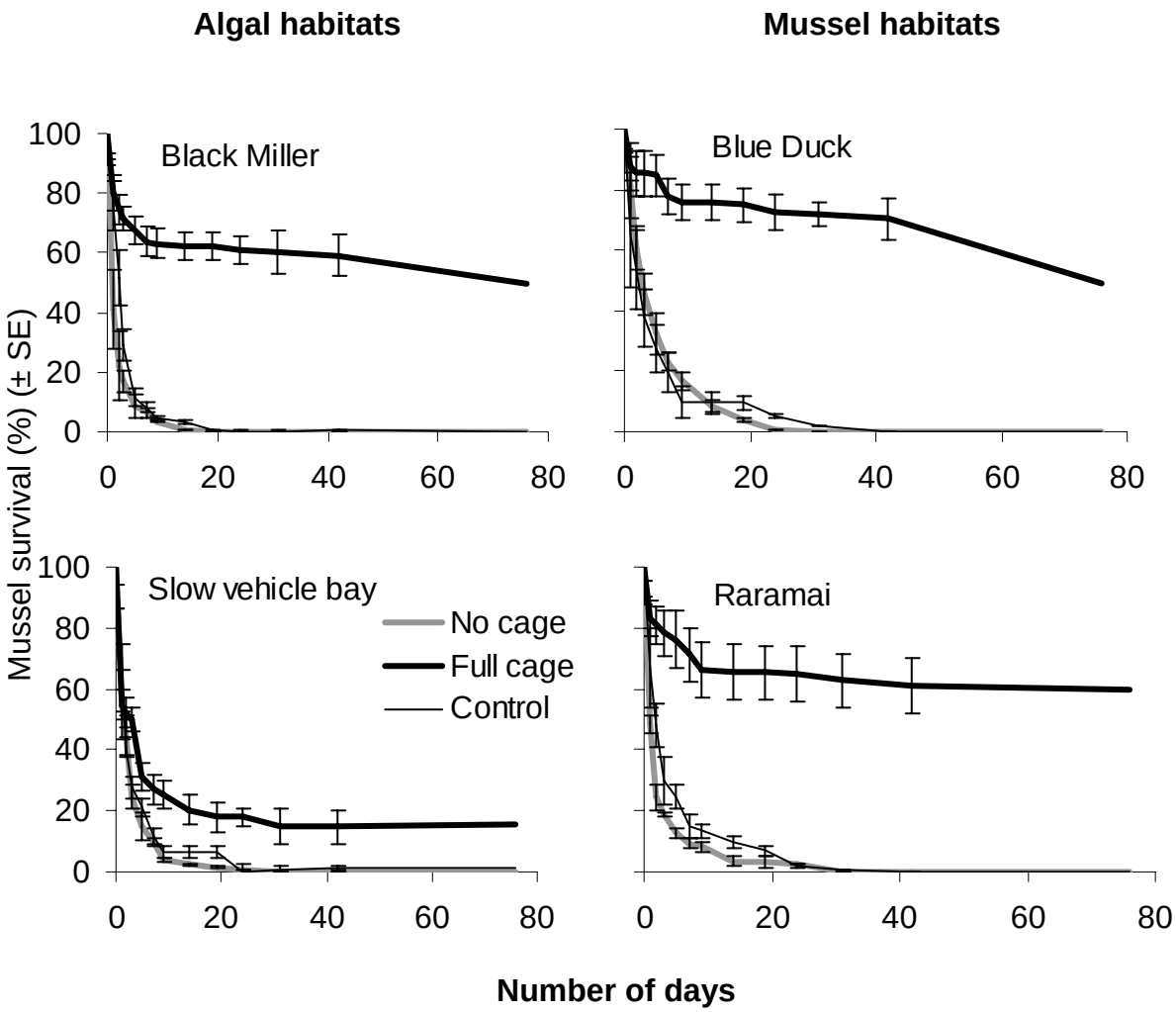

Figure 4.3 *Xenostrobus* mid-shore predation experiment. Percentage survival (mean ±SE) of small mussels (≤ 1cm) exposed to all predators (no cage), exposed to no predators (full cage) and a cage control (control) at sites dominated by algae (Black Miller, Slow Vehicle Bay) and sites dominated by mussels (Blue Duck, Raramai) in December-February 2006.

There was a significant difference between habitats in the growth of *Xenostrobus* in the low-shore cages from August 2005 to March 2005 (Table 4.5). Mussel growth was greatest at Blue Duck and this was followed closely by Raramai (Figure 4.4). No mussels survived at the two algal sites beyond December 2005, so growth measurements could not be made.

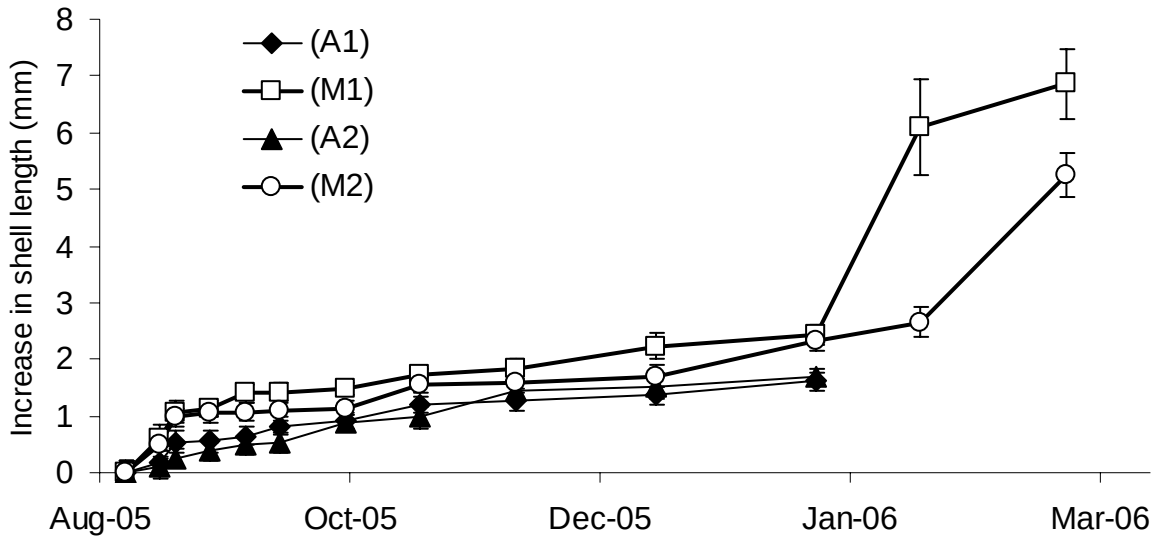

Figure 4.4 Average *Xenostrobus* growth, measured as increase in shell length (mm), across the four sites through time.

Table 4.5 Nested ANOVA on the shell length of *Xenostrobus* mussels in December between habitats (algal, mussel) and sites (nested within habitats: Black Miller (A1), Blue Duck (M1), Slow Vehicle Bay (A2), Raramai (M2)).

Source of variance	df	MS	F	P
Habitat	1	3.353	40.03	**0.024***
Site (Habitat)	2	0.084	0.12	0.883
Error	96	0.674		

Between September and January, the time when experiments were running, *Stichaster australis* were most abundant at Black Miller and Raramai (Figure 3.5). However, their overall abundance was low and they were observed consuming mussels only at Raramai.

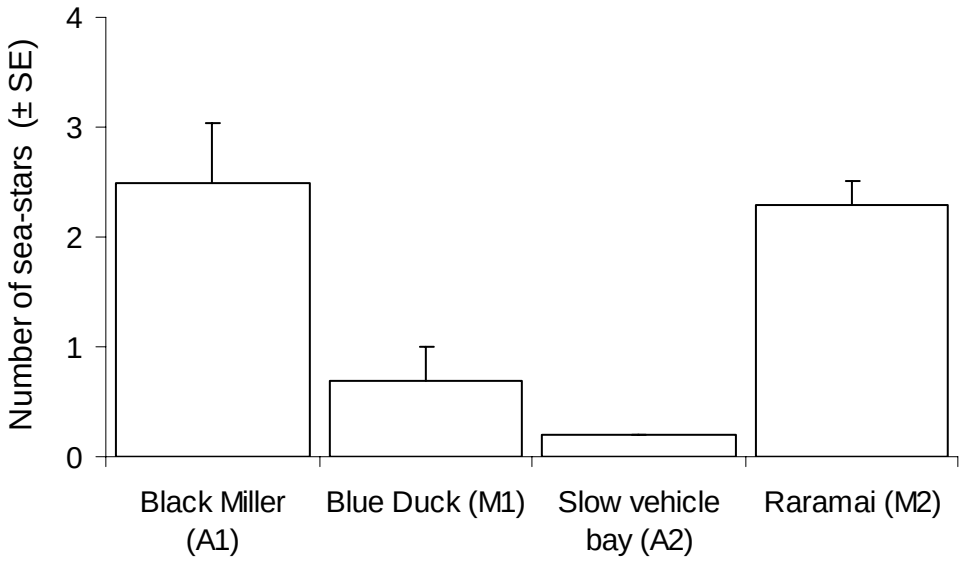

Figure 4.5 The average number of the sea-star *Stichaster australis* found at each site over four months from September to January 2006.

4.4 Discussion

Although mussel predation was rapid there was no significant difference overall between mussel survival at algal and mussel habitats. Predation was swift and effective at all sites, but did not appear to be the driver behind the different habitat assemblages in Kaikoura. However, there was a significant difference between the growth of transplanted *Xenostrobus pulex* in low shore cages at mussel and algal dominated habitats. Mussel growth was greatest at mussel dominated habitats, but after 6 months mussels from both algal habitats died.

Experiments testing the rate of mussel removal from algal habitats have not been used as a means of testing the mechanisms for the establishment of mussel dominated habitats (Schiel 2004). However, rates of mussel removal from mussel dominated habitats from sheltered to highly exposed shores have been tested extensively (Menge 1976, Menge 1978, Menge 1983, Menge and Sutherland 1987, Petraitis 1987, Barkai and Branch 1988, Petraitis 1990, 1991, Petraitis 1998, Connolly and Roughgarden 1999, Patrick 2001, Petraitis et al. 2003, Rilov and Schiel 2006).

Whelks and birds were suggested by Menge et al. (1999) to have the strongest impacts on mussels on east coast rocky-shore. However, whelk predation on mussels in southern New Zealand has been shown to be slow and inefficient and they are unlikely to have been important in my study because no drill holes were found in mussel shells and no whelks were observed in cages (Patrick 2001). Furthermore whelks are not as abundant around Kaikoura during low tide as on the shores of Maine and Nova Scotia where they are known to have strong effects on community composition (Menge 1976, Hunt and Schiebling 1998, Petraitis 1998, Patrick 2001).

The importance of bird predation has also been considered to be minor because of their seasonal presence and low abundances (Marsh 1986). In my study there was greater survival of mussels in the mid-shore compared to the low shore, suggesting that bird predation at these sites may not be influential. Large colonies of gulls are

present in Kaikoura and work done by Patrick (2001) showed that their predation on mussels, combined with oyster catchers (*Haemotopus ostralegus finschi* and *H. unicolor*), was not correlated with wave-exposure gradients, but greater predation from these sea birds was found above mid-shore levels (Patrick 2001). His work showed that oyster catchers were the most common bird predators and had significant effects on mussel survival, especially in the high-shore (Patrick 2001). While birds not seem to be as important predators in my low- and mid-shore experiments their effects on mussel populations require further study.

Mobile marine predators may be more important in determining intertidal community structure than once thought. Rilov and Schiel (2006) found that mobile predators such as fish and crabs, abundant on areas with subtidal reefs, prey extensively on intertidal mussel beds. Multiple gut contents of one species of labrid fish (*Notolabrus fucicola*) from the Kaikoura Peninsula showed that the greatest component of their diet was made up of mussels (Denny and Schiel 2001). Fish predation is likely to be the main cause of such swift mussel removal from transplanted plates. Other predators such as sea-stars are significant predators on West Coast and North Island shores, but their impact on east coast shores seems negligible because their abundance is limited (Paine 1971, Paine et al. 1985, Menge et al. 1999, Rilov and Schiel 2006). No pattern was found between the abundance of sea-stars (*Stichaster australis)* and the presence of mussel communities on east coast Kaikoura shores but their role in controlling mussels in these habitats requires more specific study.

Mussels used in my transplant experiments were less than 10mm in length. It has been suggested that a greater emphasis in predation experiments needs to be placed on early life stages (Schiel 2004) as mussels of a greater length would have shells that are more resistant to predation. Work done by Menge et al. (1999) used transplanted mussels that were relatively large (30-50mm) and found that predation intensity was low on the east coast. Sea-stars were mostly absent and crabs and whelks were considered to be ineffective predators in these areas. However, the ability to ascertain the actual top-down strength of these predators requires experiments with earlier life stages of mussels because larger ones may have already attained a size refuge from

predation by many smaller predators (Schiel 2004). The idea of a 'size refuge' was also examined by Paine (1974) who looked at the predator-prey body size relationship between *Mytilus* and *Pisaster* in Washington. He found an upper limit to the *Mytilus* size that a particular size sea-star could consume and that the upper limit was larger as the body size of the predator increased. My transplant experiments give an indication of the strength of top-down interactions between predators and prey because the mussels used were at a size where they were more susceptible to predation.

The locations in this study were selected for their seemingly similar physical aspects. All sites used in these experiments had extensive subtidal reefs, which have been various types of mobile fish and crabs that prey on intertidal mussels (Rilov and Schiel 2006). However, one site, Slow Vehicle Bay, seemed to be susceptible to faster rates of predation when compared to mussel survival times at other sites. This site, although chosen because of its physical similarities (i.e. shore height, aspect, wave-exposure) does appear to have more heterogeneous rock. Consequently, it had a greater number of intertidal rock pools and subtidal reefs. This may have had a significant bearing fish predation and may have increased the rate of mussel removal from this site.

Rates of predation at all sites, independent of habitat type, were fast and most likely the result of mobile predators such as fish and crabs. Generally, the maintenance of spatial dominance in a community is thought to be a balance between the rates of recruitment and mortality due to factors such as predation and competition (Petraitis 1995). However, sessile organisms can dominate space on rocky surfaces as many juveniles or a few large adults. Petraitis (1995) suggested that the co-variation of body size and density of a mussel bed implies that growth rate plays an important role in determining the persistence of spatial dominance by a single species. In my study I found that mussel growth rates were significantly different between habitats. Mussels transplanted into mussel habitats grew faster than the mussels that were transplanted into algal habitats, and after 6 months of growth in algal habitats all mussels died suddenly. Many factors are known to affect growth of mussels. Among the environmental conditions that are key determinants of population structure in mussels, temperature and aerial exposure are suggested to be the most important (Steffani and Branch 2003).

However, in my study, mussels that were transplanted into algal and mussel habitats were placed at similar shore heights with similar temperature regimes suggesting that other factors like food availability or food quality may influence the growth of mussels in these habitats.

The quality and quantity of food in nearshore waters are known to affect mussel growth. Gardner (2000) investigated the importance of seston (particulate matter) quality during late-summer conditions and subsequent effects on growth of three mussel species. He hypothesised that low concentrations of food would cause mussels to lose energy faster than they could gain it. As a result, mussels would be absent from areas with low seston quality (Island Bay) and present in locations with high food quality (Mahanga Bay). He found that pseudo-faecal enrichment of the water column at the mussel dominated site led to greater seston quality that was not found in the bay without mussels. The scope for growth of mussels (Hatton et al. 2005) during summer was, therefore, negative in the bay that had low seston quality and positive in the enriched waters, although this pattern did not occur year round. During winter, *Aulacomya ater maoriana* and *Perna canaliculus* had a positive scope for growth in the bay with no mussels. Mussels used in my growth experiments showed significantly different responses in habitats with and without mussels and death occurred in late summer for all mussels in algal dominated habitats. Increases in growth rates may allow mussels to reach a size refuge from predation faster and may tip the balance in determining the establishment of mussel populations at these sites. Local sources of water enrichment may be more important in determining mussel distribution than originally thought and more work is needed to understand how seston quality may affect mussel distribution on these shores.

4.5 Conclusion

No significant difference was found between mussel survival on transplanted plates at mussel and algal dominated habitats. Predation was immediate and most likely the result of mobile predators such as fish and crabs. However, no differences in removal times were found between algal and mussel dominated habitats suggesting that predation intensity is not the main determinant of algae versus mussel habitats around Kaikoura. Mean growth of *X. pulex* at mussel dominated habitats was greater than at algal dominated habitats and all transplanted *X.pulex* died suddenly at algal habitats. A fine balance between mussel removal rates and the factors that permit growth, facilitate the persistence of mussel beds in these areas.

5.1 General Discussion

The interactions of physical and biological processes are known to generate spatial and temporal patterns in natural assemblages of species and understanding the relationship between these physical and biological processes and the scales at which these interactions take place is important to ecology (Menge & Sutherland 1987, Benedetti-Cecchi et al. 2000). Caley (1996) asked the question, “to what extent does the abundance in natural populations depend on recruitment, that process which establishes initial patterns, in comparison to factors such as competition, predation, facilitation or disturbance, the processes which modify these patterns?”.

Two main hypotheses have been suggested to explain the processes that tip the balance between the domination of filter-feeders and algae across shores. The first involves the intensity of recruitment and how this intensity translates into the amount of free space and abundance of adult invertebrates in a community. The second hypothesis is derived from observations of predators determining prey distribution in both small scale zonation patterns (Witman 1987) as well as larger scale removal from areas (Paine 1971). Predators and herbivores not only limit their preferred prey (mussels) but also allow the competitors of the preferred prey (algae) to persist (Petraitis 1995).This study developed as a result of the observations of interspersed dominance of mussels on rocky-shore platforms at sites near Kaikoura on the East Coast of the South Island. I examined the idea that the absence of mussels may be a consequence of recruitment limitation but if mussels arrived at algal dominated sites, their ability to survive and grow.

The processes responsible for variation in recruitment of filter-feeding invertebrates like mussels and barnacles have been the focus of many experimental studies (Barkai & Branch 1988, Roughgarden et al. 1994, Anderson & Underwood 1997, Connolly & Roughgarden 1999, Pineda 2000, Bradbury & Snelgrove 2001, Connolly et al. 2001, Alfaro & Jeffs 2003, Gilg & Hilbish 2003, Kinlan & Gaines 2003, McCulloch & Shanks

2003, Menge et al. 2003, Guizien et al. 2006). In New Zealand, the Southland current moves north-easterly along the east cost of the South Island guided by the subantarctic convergence (Menge et al. 1999). The northward movement of this current together with onshore movement via Ekman transport have been provided as evidence that the prevailing conditions for the east coast of the South Island support downwelling (Menge et al. 1999). The absence of a thermal gradient in satellite imagery of the east coast reinforces this concept of downwelling (Vincent & Howard-Williams 1991). In Kaikoura, Chiswell and Schiel (2001) showed that the sharp temperature drops associated with upwelling were found only in summer and correlated with along-shore advection at 5m depths, but at 1m depths temperature was not in phase with wind. Menge (1999) suggested that east coast conditions would eventually drive larvae to deeper depths offshore and limit phytoplankton concentrations needed for mussel growth. Bivalve larvae have a preferred temperature range, but their movement in the water column has always been assumed to be passive following water movement via thermal gradients and upwelling and downwelling events (Scheltema 1986). More recently, Genin (2005) found that zooplankters were able to control their vertical distribution in the water column by swimming against upwelling and downwelling currents, but were carried passively with horizontal flow. However, Shanks (2005) has looked at the species-specific nature of upwelling/ downwelling effects on larval settlement and suggests that if mussels are actively able to control their vertical distribution then mussel larvae could return to shore regardless of the upwelling/ downwelling nature of the nearshore water mass.

Life histories of species and their relationships with processes such as upwelling and downwelling, oceanic conditions, larval arrival and settlement processes have also been a major focus of ecologists investigating how invertebrate communities are maintained (Schiel 2004). Dispersal during a 2-3 week planktonic phase in duration can transport mussel larvae several hundred kilometres (Pineda 2000). Consequently recruitment to a section of a shore is likely to be from larvae that originated elsewhere. Gaines and Roughgarden (Gaines & Roughgarden 1985) noted that larval settlement rate is of utmost importance in population dynamics as the generalisations about the role of competition in causing patterns of zonation and the ‘intermediate disturbance

hypothesis only seem to be relevant when settlement rates are high. However, the examination of community dynamics have rarely been done when recruitment intensity is low and adult abundance is high. Mussel habitats around Kaikoura are an example of this. Recruitment of all species of mussels to tuffies was not found to be significantly different between mussel and algal habitats yet small populations of mussels persist at particular sites and not at others. The consistent settlement of recruits year round onto the shore was also reflected in the steady numbers of mussels found in core samples taken from adult mussel beds at mussel dominated sites. How these levels compare with recruitment at other east coast shores is important to understanding the mechanisms behind their persistence. At east coast Banks Peninsula sites, Menge et al. (1999) also found consistently low mussel recruitment from November 1994 to April 1995. Sites similar to Menge et al. (1999) were also used by Rilov and Schiel (2006) and mussel recruitment was found to be on a similar scale. However, according to the mean recruitment of four species of mussels into collectors at sites without contiguous subtidal reefs in April 2003, they found that thousands of mussels had recruited. Although the results obtained in this study were from a small time scale this large influx of recruits gives an indication of the high concentrations of mussel larvae that are present in larval pools on the east coast. Recruitment is limited in Kaikoura but by no means is it the only limiting factor determining the spatial distribution of mussels. Recruitment was found to be low but consistent at all sites so the importance of recruitment determining local population size cannot be deciphered by measuring recruitment rates alone; additional knowledge of mortality patterns are also required (Petraitis 1998).

Osman (2004) found that on small isolated substrates, predation on newly settled individuals has the potential to control recruitment, regardless of larval supply. The mortality of mussels can be the result of many factors, including predation (Menge 1978a), competition (Paine 1974), or a host of environmental limitations (Menge 1976). Predatory invertebrate species are in short supply on the east coast of New Zealand and predation pressure on these shores is a result of varying levels of predation by groups including whelks (Fairweather et al. 1984, Navarette 1996, Hunt & Schiebling 1998, Petraitis 1998), sea-stars (Laudien & Wahl 1999), birds (Baird et al. 1985,

Wootton 1997, Patrick 2001) and fish (Denny & Schiel 2001, Morrisey et al. 2006, Rilov & Schiel 2006). In other temperate locations invertebrates like gastropods have been found to be the most important predators on many shores. For example *Thais lapillus* was the cause of the low abundance of mussels and barnacles from sheltered shores in New England (Menge 1976). However, studies done by Patrick (2001) and Rilov and Schiel (2005) in New Zealand showed that mobile predators have a greater impact on temperate shores on the east coast with both suggesting that fish, especially where intertidal platforms are contiguous with intertidal reefs, may be a significant component of the suite of predators on the east coast.

Findings similar to those by Rilov and Schiel (2006) were found at sites near Kaikoura where mussels were removed from uncaged treatments at all sites within the first couple of days, regardless of the types of species that were dominating the habitat. This rapid removal is most likely the result of predation by mobile predators as the time between location of prey and the commencement of drilling by whelks, which is known to leave behind empty shells, is known to take at least four days (Petraitis 1998). This fast predation rate of mussels from uncaged treatments operated at a local scale within sites as well as between sites indicating that similar species are responsible for the removal of mussels from both algal and mussel habitats. All sites were located within several metres of subtidal reefs, within the home range of several species of mobile fish predators (Denny & Schiel 2001), which may have facilitated this fast predation rate.

Mid-shore predation rates were lower than low-shore rates suggesting that bird predation is not a significant factor in this system (Marsh 1986). However, rates of predation were similar between sites independent of the presence or absence of algae and mussels. Variations in intensity of predation and recruitment were not found to be the basis governing the absence of mussels from algal dominated shores. However, growth rates of juvenile transplanted *Xenostrobus pulex* were found to be significantly different between algal and mussel habitats.

Petraitis (1995) addressed the importance of growth in prolonging the persistence of mussel beds. He developed a model which linked percent cover of mussels to growth, recruitment and mortality. He found that over the short term, mussels suffer from a large number of deaths and persist without any change in percent cover, provided the remaining mussels can grow fast enough to fill the vacated space. He suggested that chronically sparse recruits may be sufficient enough to replenish the beds as long as they grow fast enough. However, if conditions do not favour growth then mussels would suffer from extensive mortality. This appears to be the case at algal dominated sites near Kaikoura. Mussel and algal dominated habitats receive sparse levels of recruits but the conditions at mussel dominated sites possibly favour faster growth rates which enable mussels to fill vacant space. Many factors are known to influence mussel growth with the most likely factor in this system being a limitation in food availability and quality.

The amount of food ingested by bivalves is dependent on the availability of food and filtration rates (Camacho et al. 1995). Mussel growth is reliant upon the quality and quantity of seston or phytoplankton concentrations. Shoreline configuration has been examined as a factor that can alter local hydrodynamics that can modify the dispersion of small suspended particles including phytoplankton (Aristegui et al. 1997). Archambault (1999) examined whether mussel growth of *Mytilus edulis* was related to shoreline configuration via phytoplankton concentration. Embayment size effects were observed for both phytoplankton concentrations and mussel growth. Larger embayments are thought to retain greater concentrations of phytoplankton explaining greater growth increments.

Dahlhoff and Menge (1996) also investigated the relationship between nearshore food availability and physiological responses of the mussel *Mytilus californianus* to gain an understanding into the mechanisms underlying variation in community structure between rocky intertidal regions. They found a strong link between the seasonal variation in the quantity of food available. There are relationships between composition of the diet and the metabolic activity of mussels. However, mussels can adjust their metabolism depending on the composition of their diet. In conjunction with the

observation that mussels respond rapidly to fluctuations in phytoplankton bottom-up effects may be a more important determinant of differences in community structure.

The theory of alternative stable states suggests that two or more different types of communities are able to occur in the same habitat. The presence of algae on Kaikoura shores in areas where mussels could persist may be an example of this. However, proving the presence of alternative stable states has been difficult (Connell & Sousa 1983). The likelihood of each community type switching would be dependent on the intensity of perturbation. Petraitis et al. (2003) suspects that the development of a mussel bed following a disturbance requires consistently good recruitment over a number of years and the successful establishment of mussels will depend on the presence and abundance of barnacles and filamentous algae, both of which have been suggested to facilitate mussel recruitment (Kitching et al. 1959, Bayne 1964, Menge 1976, Petraitis 1987, 1990). Barnacles may also improve mussel survivorship by diverting predators from mussels and onto barnacles (Fairweather et al. 1984, Petraitis 1987). They also suggest that the establishment of mussel patches which persist for the long-term will depend on the size of the mussel bed and the ability to sustain itself and resist invasion (Petraitis 1995). Mussel beds in habitats around Kaikoura seem to have a slight edge in survival and growth over other locations. Greater resources for survival and growth, and a slightly larger accumulation of recruits through time at mussel dominated habitats, have facilitated the persistence of mussel beds around Kaikoura.

5.1 Conclusion

Recruitment of all mussel species was found to be consistently low at all sites. Recruit sized mussels were collected at all sites year round. However, the absence of mussels from algal dominated habitats does not appear to be a result of recruitment limitation. Experiments examining transplanted mussel removal from algal and mussel dominated habitats showed that predation was likely to be the greatest cause of mussel removal from sites. However, rates of mussel removal were not significantly different between

habitats. This suggests that variation in the intensity of mussel predation between algal and dominated habitats does not restrict the distribution of mussels. A significant difference was found between habitats in the growth rates of *Xenostrobus pulex*. The culmination of small numbers of recruits through time and a fine balance between rates of survival and growth seem to be responsible for the persistence of mussel beds at specific sites around Kaikoura.

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